The influence of savannah elephants on vegetation: a case study in the Tembe Elephant Park, South Africa

by

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The influence of savannah elephants on vegetation: a case study in the Tembe Elephant Park, South Africa

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Abstract

Most elephants in South Africa live in enclosed areas such as the Tembe Elephant Park in Maputaland. The Park also protects sand forest. This can create a conflict of interest as elephants may influence species typical of these forests. To assess the effects that elephants may have for vegetation, I compare variables of similar plant communities inside and outside the Park. I then compared the space and landscape utilization of elephants living in the Park with those of free-ranging elephants living in southern Mozambique. In the final analyses, I used meta-analytical methods to interpret my findings.

Woody seedlings showed no measurable response to tree canopies that elephants have altered, but the response of grasses and woody saplings depended on the landscape type. In closed woodlands, elephants generated gaps in the canopy layer that increased structural heterogeneity. These gaps favoured the establishment of grasses, and along with herbivory, may have been responsible for reduced occurrence of woody saplings. In the open woodlands, elephants and frequent hot fires in the Park apparently homogenised this landscape. In this case, altered tree canopies reduced grass and woody sapling presence.

The species compositions of sand forests, closed woodlands and open woodlands between inside and outside the Park differed. However, tree and shrub densities, their abundance-incidence and rank-abundance relationships were similar for a given landscape inside and outside the Park. Ecological events operating at larger scales, such as seed dispersal and droughts, mask the influence elephant have for these community variables.

Elephants in the Park had smaller home ranges than free-ranging elephants living in southern Mozambique. The size of these home ranges were however, similar to that predicted by rainfall, as suggested by my analysis of data collected across southern Africa. The elephants that roamed freely in southern Mozambique prefer closed woodlands throughout the year. However, elephants confined to the Park avoided reed beds (with natural surface water) in the dry season and showed no landscape preference in the wet season.

My meta-analysis on the effects of elephants on other taxa included 230 peer-reviewed studies. These were published over a 40-year period and included information from 74 sites. From only those studies used in the effect size calculations, when conducted over a period of less than 5 years show a negative impact while those conducted over longer periods show a neutral effect. Site-specific differences, such as rainfall, may also influence the effect elephants have for plants. Twenty of the 230 studies shared more than 50% of all citings. The majority (16 of the 20) claimed that

elephants had a negative influence for plants. This is in contrast with the findings of all studies included in the analysis – half of these concluded a positive effect and the other half a negative effect. In short, elephants do not decrease the diversity of other species present in the system, despite their adverse effects for individual trees. Elephants affect ecosystems at small scales. Providing an opportunity for elephants presently living in Tembe Elephant Park to disperse across their former ranges may negate negative influences on sensitive vegetation in the Park.

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First, I would like to thank Rudi van Aarde. Thank you for your trust, support and patience in me over the last number of years. A few sentences cannot express my appreciation for the faith you have shown in me and in believing that I will be able to complete this work. In addition, I value your shaping my thoughts on conservation, ecological restoration and management philosophy. Your interpretation of these topics, all very close to my heart, will influence my future career. Weereens – Baie Dankie Rudi.

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Disclaimer

The present dissertation includes four paper manuscripts, prepared for submission to different scientific peer-reviewed journals. Styles and formatting of these chapters follow the respective journal requirements. This results in some duplication in study site description and methods between chapters. Chapters 1, 2, 7 and the Appendices follow the format requirements for the *Journal of Ecology*. I compiled a single Reference list for Chapters 1, 2 and 7 and follows directly after the Synthesis. I hereby declare all the work to be my own and that I have acknowledged all those that helped me and contributed in producing this dissertation.

Robert AR Guldemond

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Chapter 1

General introduction

The influence of elephants (*Loxodonta africana* Blumenbach, 1797) on biological diversity is of conservation significance (e.g. Cumming *et al*. 1997; Trollope *et al*. 1998; van de Vijver *et al*. 1999; Whyte *et al*. 2003; Wiseman *et al*. 2004; Goheen *et al*. 2004; Skarpe *et al*. 2004). This is particularly true where elephants are confined, and even more so, when protected areas are small and support sensitive vegetation. The Tembe Elephant Park (TEP) in northern KwaZulu-Natal, South Africa, presents such a scenario.

TEP is one of two conservation areas in the Maputaland Centre of Endemism (van Wyk 1996) that support remnants of a previously widely distributed elephant population (see Morley 2005). The other conservation area is the 'Reserva Especial de Maputo' (here after; the Maputo Elephant Reserve [MER]) situated in southern Mozambique. Maputaland is known for its species richness and high levels of endemism (e.g. Küper *et al*. 2004) and has recently been recognised as part of the Maputaland-Pondoland-Albany biodiversity hotspot (www.biodiversityhotspots.org). Conservation in Maputaland stands to be affected by these developments, not only inside but also outside formal conservation areas (Reid 1998; Myers *et al*. 2000; Cincotta *et al*. 2000).

The TEP is fenced, small (300 km^2), and supports a unique sand forest ecotype that contributes greatly to the overall levels of endemism (Kirkwood & Midgley 1999; van Rensburg *et al*. 1999, 2000; Matthews *et al*. 2001). The fencing of the Park made intuitive sense to conservation authorities that wanted to protect these forests from human-induced damage (Sandwith 1997). The authorities also wanted to prevent elephant poaching, and limit elephant contact with humans. However, confining elephants to the Park may create a new conflict, should they destroy the sand forests, and negatively affect the associated endemic species (e.g. Kirkwood & Midgley 1999; van Rensburg *et al*. 1999, 2000; Matthews *et al*. 2001; McGeoch *et al*. 2002).

Not all of the elephants living in Maputaland are restricted to conservation areas. The MER in southern Mozambique is unfenced and elephants living here roam freely onto communal lands along the Futi River (de Boer & Baquete 1998; de Boer *et al*. 2000; Soto *et al*. 2001) that extends all the way to the TEP.

The restriction of range use by elephants is not the only human-induced problem that the managers of the TEP may face. The establishment of artificial water sources represents another disturbance, since it may alter the way elephants use landscapes and vegetation (e.g. de Beer *et al*. in press). Furthermore, it affects elephant demography (Shrader *et al*. in review), adding to the disruptive effects elephants may have for the ecosystem. This scenario is not unique to the Tembe Elephant Park, as most elephant populations across South Africa are confined by fences to areas less then 1 000 km^2, where their numbers increase at rates exceeding 7% per year (see Slotow *et al*. 2005).

In 2000, the Conservation Ecology Research Unit (University of Pretoria) initiated a number of studies focussing on Maputaland's elephants. The research programme was directed at investigating the consequences of fragmentation for this elephant population and for the landscapes where they live. My study deals specifically with the consequences that elephant confinement may have for the vegetation of the Tembe Elephant Park. My study aims to contribute to the future management of elephants in Maputaland and elsewhere.

Elephants in Africa are closely linked to conservation issues. Here, some consider elephants as flagship species (Western 1987), while others treat them as umbrella or focal species (e.g. Roberge & Angelstam 2004) and project them as icons for conservation. The underlying premise is that biological diversity will benefit when suitable areas are set aside for the protection of elephants (Caro & O'Doherty 1999). Elephants are also considered by some as a keystone species (Power *et al*. 1996), a term that often extends to 'ecological engineers' (Jones *et al*. 1994). This implies that their removal from a system may have consequences for other components (Mills *et al*. 1993). The concept also implies that elephants have the capacity to transform their environment and manipulate the living conditions for other species (Jones *et al*. 1994; Power *et al*. 1996).

The savanna biome, in which my study area is situated, is characterised by the coexistence of herbaceous and woody plants (Walker & Noy-Meir 1982; Belsky 1990). This biome is inherently complex and continuously in varying states of flux between different stable states (e.g. Walker *et al*. 1981; Noy-Meir 1982; Gillson 2004; Ssemanda *et al*. 2005). Previous reviews (Scholes & Archer 1997; House *et al*. 2003; Sankaran *et al*. 2004) summarised the various models that describe coexistence between grasses and trees and concluded that spatio-temporal scales (e.g. Levin 1992) are key to explanations of the mechanisms that maintain savanna systems. These mechanisms may include competition-based (niche separation, balanced competition, alternate stable states) and demographic-bottleneck models (the 'storage effect') (House *et al*. 2003; Sankaran *et al*. 2004). Ecological events, such as disturbances caused by fire and herbivory may further influence these mechanisms that affect tree densities and shift savanna systems from woody to grasslands states (Dublin *et al*. 1990; Prins & van der Jeugd 1993; van de Koppel & Prins 1998; Bond *et al*. 2005). The role that elephants play in savannas links closely with other disturbance events, consequently fire and other herbivores, other than elephants, may either mask or amplify the signals of impact left by elephants in areas such as TEP.

I studied the impact elephants may have had on vegetation by following the hierarchical approach by investigating responses at increasing spatio-temporal scales (see Allan & Starr 1982; O'Neil *et al*. 1987). This allowed me to identify the level at which elephants influence the vegetation and how prevailing conditions in the TEP determined the outcomes of the study. I compared plant community variables of areas with and without elephants, and compared space and landscape utilization of elephants in the Park with those of free ranging elephants in southern Mozambique. However, elephants are not the only agents that may influence some of the response variables I measure. Other browsers and fire, may also affect plant species in the Park, but elephants dominate the browsing guild. I therefore often refer to the "Park effect" to accommodate the disturbance role that other browsers and fire, in conjunction with elephants may have on plants.

My dissertation comprises three sections. In the first section (Chapters 1 and 2), I provide a general introduction and describe the study area. The second section (Chapters 3 to 6) provides the scientific content of the study. The first of these chapters addresses the effects elephants may have for plants in the TEP at the smallest scale, followed by separate assessments in the following chapters, each with increasing spatio-temporal scales. In the third section (Chapter 7), I synthesise my findings, and reflect on relevance thereof to elephant management in the TEP.

In Chapter 3, I focus on the effects of elephants on the canopies of tree species that are high in their dietary preference in TEP. I also study how the sub-canopy vegetation associated with these trees may respond to changes in canopy structure. Previous studies on the feeding behaviour of elephants suggest that they alter tree canopies by breaking branches and/ or displacing entire trees (e.g. Barnes 1982; Lewis 1986; Jachmann & Croes 1991). My research takes this one step further by looking at the community level response as reflected by diversity and evenness indices of grasses, woody seedlings and saplings associated with these altered tree canopies.

At the intermediate scale (Chapter 4), I investigate how the different landscape types (open woodlands, closed woodlands and sand forests) responded to the presence of elephants and the other species living in the Park. Here, I compare densities, species composition, abundance-incidence and species rank-abundance relationships of trees and shrubs noted in the different landscapes inside the Park with those recorded in similar landscapes outside the Park.

At the macro scale (Chapter 5), I focus on space use and landscape selection patterns by elephants in Maputaland. As elephants are fenced in and provided with artificial water, I expected that their use of space in TEP would differ from that of free roaming elephants living in the Maputo Elephant Reserve and along the Futi River Corridor in southern Mozambique. I collected elephant location data provided by satellite collars and projected these onto landscape types derived from satellite images of the region.

To assess the apparent impact of elephants, and to place the impact of elephants in the TEP into a continental context, I performed a meta-analysis on the consequences elephants have for plants, other vertebrates and insects (Chapter 6). A meta-analysis is a quantitative assessment that uses statistical techniques designed to combine the results from different studies to evaluate the overall effect size (Cooper & Hedges 1993). In this case, the overall effect size is the consequences elephants have on other taxa present in the system. This procedure allowed me to partition out possible explanatory variables relating the overall effect of elephant and to identify the shortcomings in the current scientific literature. This meta-analytical procedure also minimizes site-specific biases in my assessment, which may lead to incorrect conclusions and management recommendations.

The study aims to investigate the consequences of the confinement of elephants may have for plants in Tembe Elephant Park. Instead of focussing on species level alone, I concentrate on the response of plants from the individual tree to the plant community level. This study also uses ‘state of the art’ remote sensing technology, such as satellite imagery and tracking of elephants to investigate their response to confinement. Finally, this study answers the question of ‘How does the current situation in Tembe Elephant Park compare with other elephant populations in Africa? Management decisions regarding elephant’s space use patterns, as oppose to elephant numbers *per se*, stand to be affected by outcomes and interpretation of my results.

Chapter 2

Study area

The study area is situated at the southern end of the Mozambique Coastal Plains. This area, now known as Maputaland, includes the Matutuine District of the Maputo Province in southern Mozambique and the northern part of the KwaZulu-Natal Province of South Africa. Geographically, the area stretches from the Lebombo Mountains in the west, the Indian Ocean in the east, the Bay of Maputo in the north and Lake St. Lucia in the south. The two conservation areas of interest include the Maputo Elephant Reserve (MER) (26°25'S, 32°45'E) and the associated Futi River Corridor (FC) in southern Mozambique, and the Tembe Elephant Park (TEP) (27°01'S 32°24'E) in South Africa (Fig. 2.1).

The MER was established in 1932 and covers some 800 km^2 under legislative protection of National Directorate for Conservation Areas (DNAC). Ezemvelo KwaZulu Natal Wildlife (EKZN), a provincial department, has the managing mandate for the TEP. The Park was proclaimed in 1983 and then fenced along its western, southern and eastern boundaries to prevent direct contact with people living on the South African side (Sandwith 1997). At 300 km^2, TEP covers an area less than half of MER. In 1989, the northern boundary with southern Mozambique was fenced off.

Some 17 people per km^2 (www.demarcation.org.za) reside mainly south and southeast of TEP, with no people living inside the Park. This differs from MER, where people remained after its proclamation (de Boer & Baquete 1998), and where they concentrate mostly in the southern and southeastern regions of the Reserve.

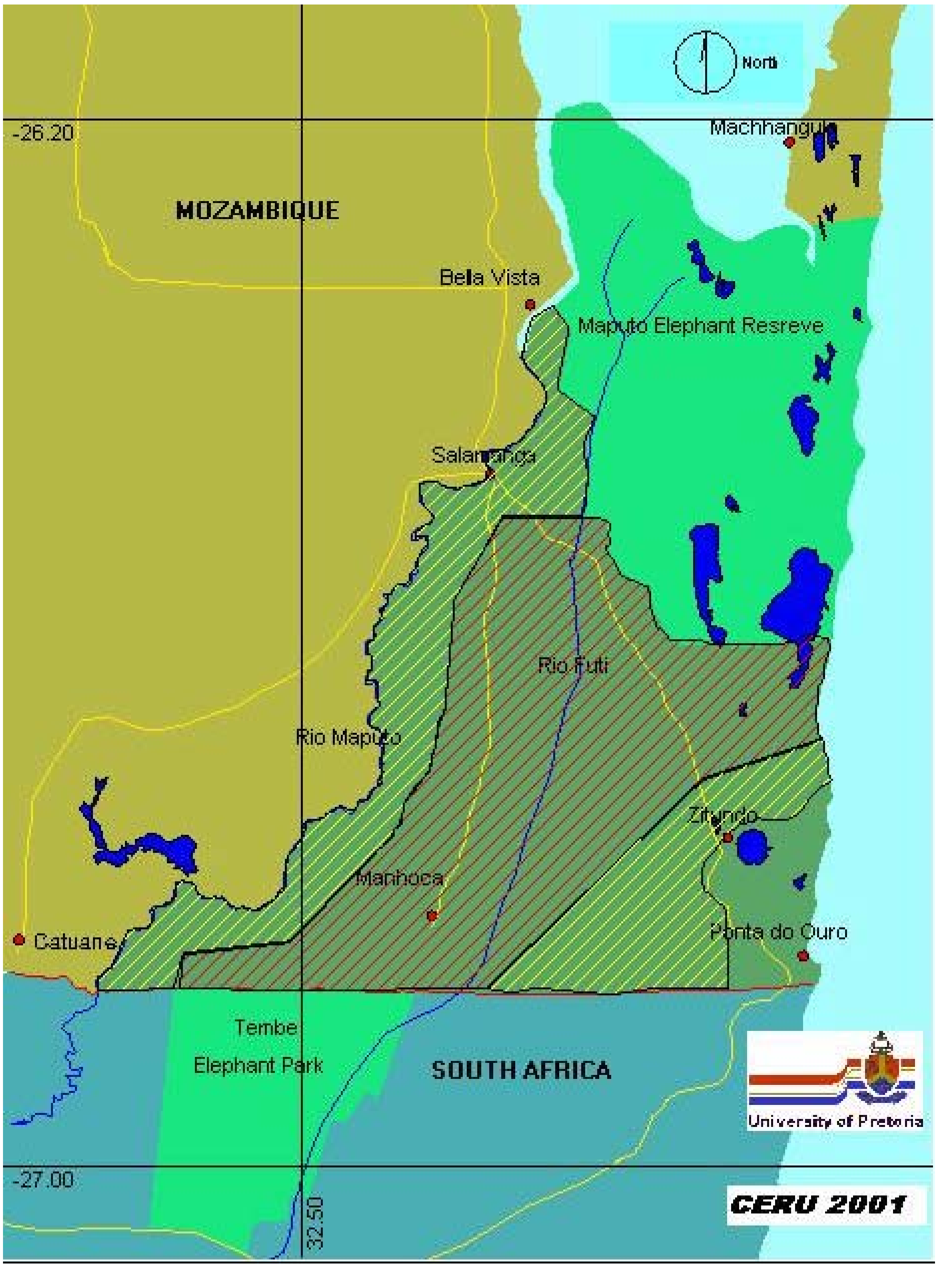

Fig. 2.1 Maputaland extends across the South African and Mozambican border. The Maputo Elephant Reserve and the Futi River are situated in southern Mozambique and Tembe Elephant Park in South Africa. The hatched area indicates the potential Futi corridor. This 40 km long strip used to link the two conservation areas before fencing the Tembe Elephant Park effectively divided this singular ecological entity in Maputaland.

The Physical Environment

The Mozambican coastal plains are covered in deep aeolian sands deposited during the quaternary period between 3 million and 10,000 years ago (Maud & Botha 2000), Geologically, this is one of the youngest landscapes in southern Africa and the soils are highly permeable, heavily leached and nutrient poor (Pollet *et al*. 1995). Along the riverine floodplains however, alluvial soils occur, with higher clay and base content (Myre 1964; Pollet *et al*. 1995). These areas are rich in organic matter. The nutrient-poor soils also alternate with clay-rich duplex soils that formed between sand dune ridges (Matthews *et al*. 2001).

The coastal plains consist of relict, north south running longitudinal dunes that extend from southern Mozambique into TEP and its surroundings. The main drainage lines consist of the Maputo and Futi Rivers, both which run in a south-north direction. The Maputo River drains in a large estuary in Maputo Bay. The Futi River originates just south of TEP, flows through the Park just inside the eastern perimeter (known here as the Muzi Swamps), and ends in the MER where it flows into a delta system. Seasonal pans occur along the Muzi Swamp, as well as between the dune ridges where either clay or duplex soil types are exposed. Other sources of surface water include several fresh water and saline lakes and marshes scattered throughout the study area.

The climate of Maputaland is sub-tropical, with hot wet summers and warm dry winters (van Wyk & Smith 2000). Humidity is high and evaporation exceeds precipitation for all months except in December, January and February (Schulze 1997). Winds are generally light with little seasonal variation in velocity. Gale force winds are recorded for the region (Pollet *et al*. 1995) and tropical cyclones are sometimes accompanied by destructive winds. No temperature data is available for southern Mozambique or TEP. The nearest reliable source is the Mbazwana Airstrip (27º28'S 32º35'E) situated 60 km southeast of TEP. Here, temperature records show that, for the duration of the study period (2001 to 2003), the monthly mean (±SD) temperature (°C) ranged from 10.6 ± 1.76 to 21.7 ± 2.35 for the daily minimum and 23.6 ± 3.22 to 31.5 ± 3.78 for the daily maximum respectively.

Two rainfall stations recorded rainfall for the region. For southern Mozambique, we used the data collected at Changalane (26º17'S 32º11'E), which is the nearest station in southern Mozambique, and for TEP at the Park's headquarters (27º01'S 32º24'E). Rainfall patterns for the sites were similar for the duration of recording period. Southern Mozambique (1980 – 2002) received a mean (±SD) amount of 757 ± 226 mm and TEP (1959 – 2002) received 748 ± 388 mm annually (Figs. 2.2a & d). The coefficient of variation for the region is high, and ranged between 25 – 30 % (Schulze 1997). The cumulative rainfall surplus/deficit (see Dunham *et al*. 2004) for both TEP and southern Mozambique followed similar patterns, and the entire region experienced a dry period before the study, and higher than average rainfall during the time of field data collection (Figs. 2.2b & e). Rain may fall throughout the year but peaks during summer with a trough in winter (Figs. 2.2c & f). Months that contributed to less than 5% of the annual rainfall range from May until September, and this is consequently considered as the dry season. The wet season (October to April) for both TEP and southern Mozambique contributed more than 80% of the annual rainfall.

The Biological Components

The region between the Maputo, the capital of Mozambique, and Lake St. Lucia in

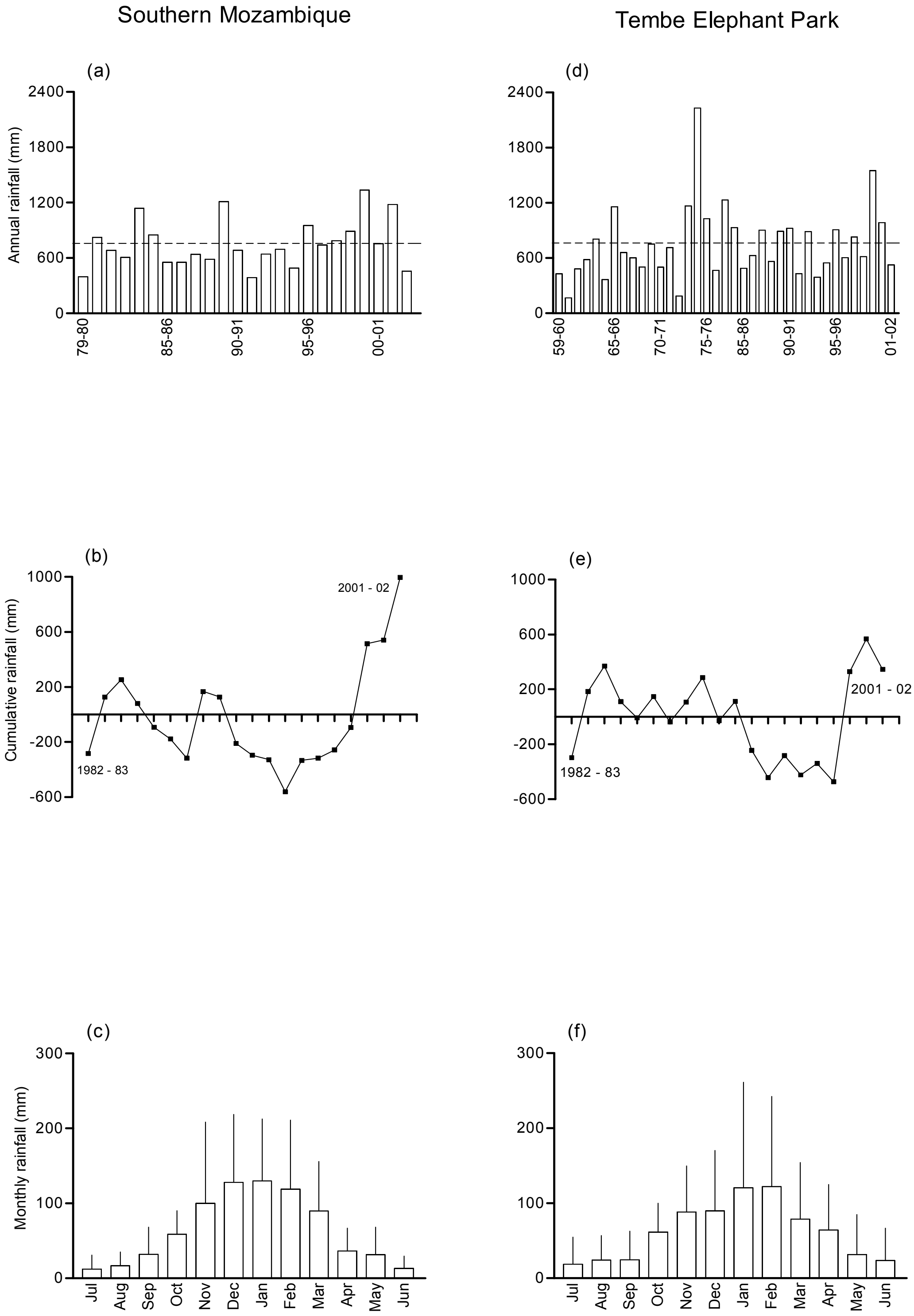

Fig 2.2 Rainfall variables for southern Mozambique and Tembe Elephant Park including (a & d) mean annual rainfall (calculated from the 1982/83 to 2001/02 season) (b & e) cumulative surplus/deficit rainfall and (c & f) mean (±SD) monthly rainfall.

South Africa represents the southern limit of the central African tropics and the northern limit of the southern African temperate forests (van Wyk 1996). This transitional zone supports plant and animal species from both the tropics and the temperate coastal regions (Moll & White 1978; Spector 2002). Van Wyk (1996) recognises this region separately as the Maputaland Centre (MC), due to high levels of diversity and endemism.

Recently Conservation International included this region into the Maputaland Pondoland-Albany Biodiversity Hotspot (www.biodiversityhotspots.org), one of 39 such regions around the world. The Maputaland regional contribution to this hotspot includes more than 2,500 species of vascular plants, 102 mammalian species/sub species and 472 bird species (Parker & de Boer 2000; Davis *et al.* 1994). Four of the bird species are endemic and 43 subspecies are either endemic or near endemic (Davis *et al.* 1994), now also recognised by BirdLife International as the Southeast African Endemic Bird Area. The region further supports a rich herpeto-fauna, with 112 species/subspecies of reptiles, 23 of which are endemic (Bruton & Haacke 1980) and 45 frog species, three of which are endemic (Poynton 1980). Some 67 species of fresh water fish occur here, of which 12 are endemic to Maputaland (Skelton 2001).

The elephant population estimate for MER and FC ranged from 80 to 350 individuals over the past 30 years (Morley 2005). The most recent estimate yielded 204 individuals (Ntumi 2002), increasing at about 3 percent per year (Morley 2005). The elephant numbers in TEP was relatively low (< 50 individuals) prior to erecting fences around TEP in 1989, but has since increased to 179 (95% CI = 136 – 233) for 2001 at 4.6 ± 0.06 percent per year (Morley 2005). These estimates yield a density of 0.25 and 0.59 elephants per km^2 for MER and TEP respectively.

Maputaland falls within the northern most part of the Tongaland–Pondoland Regional Mosaic, one of the main African phytochoria described by White (1983). The landscape of Maputaland is heterogeneous, and may be described using different classifying criteria (e.g. Moll & White 1978; Acocks 1988; Granger 1998). For instance, de Boer *et al*. (2000) recognises six plant communities within the MER and Matthews, *et al*. (2001) distinguished eight physiognomic vegetation types for TEP. The study area is however situated in the savanna biome (Westfall & Rutherford 1994), characterised by the coexistence of trees and grasses.

I define the landscape of the study area based on the structure of trees and shrubs (adapted from Edwards 1983). Such structures reflect on function since it relates to the physiological needs of elephants (e.g. Laws *et al*. 1970; Kinahan *et al*. in review). I used the classifications by de Boer *et al*. (2000) and Matthews *et al*. (2001) to verify the four broad landscape types (based on the landscape map constructed by Fairall & van Aarde (2004), using a cloud free partial scene ID 167-79 of 30 August 1999, Fig. 2.3). These included forests (mainly sand forest, and some swamp- and coastal dune forests), the open and closed woodlands and reed beds. Sand forests are very dense and a dry semi-deciduous forest type (van Wyk 1996). The closed woodlands are characterised by a closed and layered canopy with very dense undergrowth. Sparsely spaced mature trees and prominent grass sward dominate the open woodlands. The reed beds (dominated by *Phragmites australis* (Cav.) Steud) are associated with the Muzi Swamp in TEP, the FC and other surface water bodies in MER.

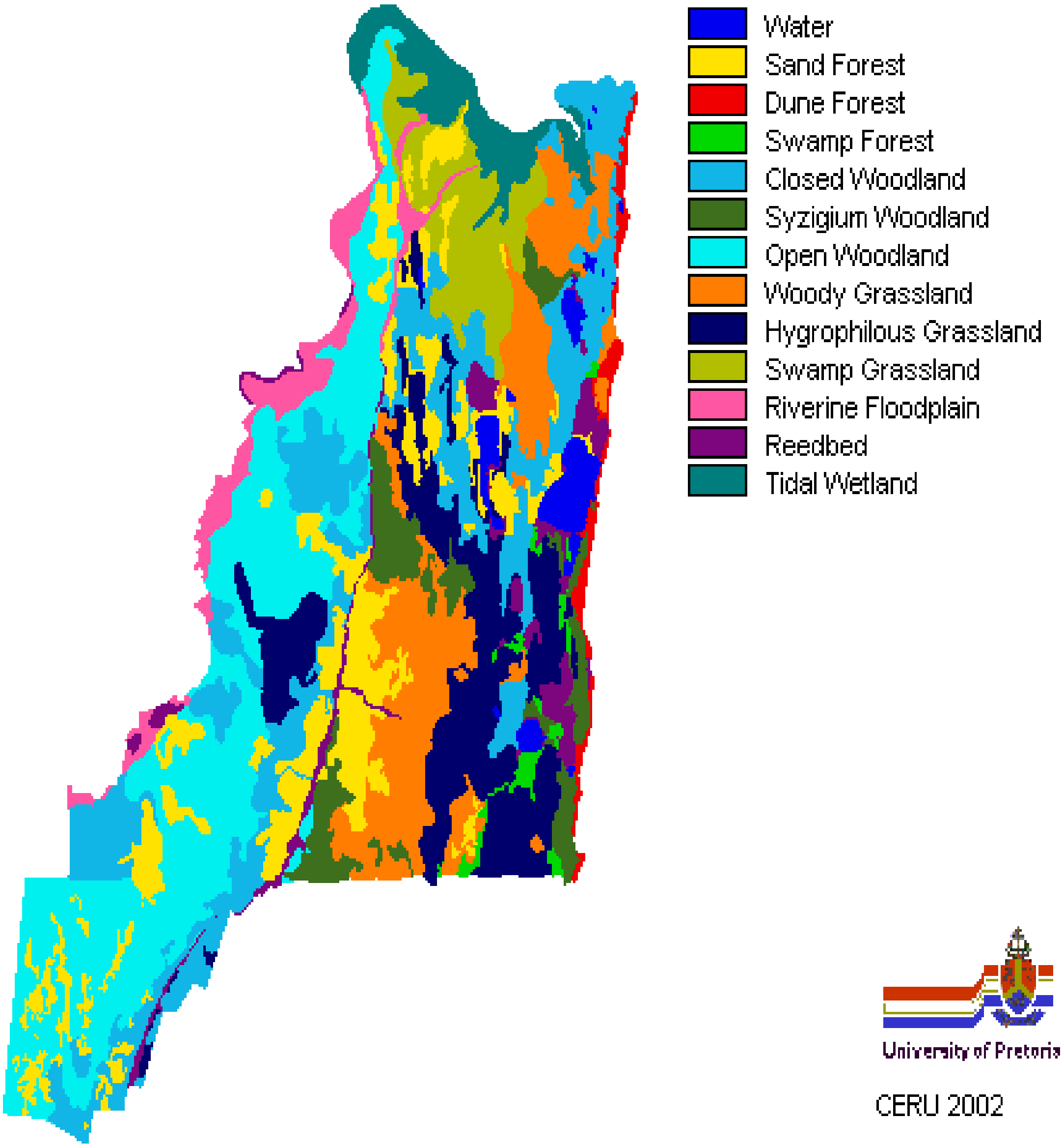

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Fig 2.3 Landscape map of Tembe Elephant Park and southern Mozambique based on a supervised classification of a LANDSAT image of the area. Ground truthing of the landscapes was based on vegetation information from de Boer *et al*. (2000) and Matthews *et al*. (2001).

Chapter 3

Manuscript prepared for submission to the Journal of Tropical Ecology

The effect of elephant-modified tree canopies on sub-canopy savanna plant communities

Robert A.R. Guldemond & Rudi J. van Aarde

Abstract

Mechanisms that sustain grass-tree coexistence in savannas rely to a large extend on the longevity of mature trees. Browsing by elephants may increase tree mortality and could alter the coexistence of grasses and trees. Elephants may therefore have consequences for savanna diversity. We assessed the changes in diversity and evenness indices for grasses, woody seedlings and saplings in response to elephant-induced canopy changes. In closed woodland, elephants generated gaps in the canopy layer that favoured grass establishment and allowed woody saplings to grow into the canopy layer. Browsing by elephants and other herbivores reduced the occurrence of woody saplings but not that of seedlings. In the open woodland reduced canopy cover did not affect the presence of seedlings, but did reduced grass and woody sapling occurrence. Elephants increase the structural heterogeneity of closed woodlands, but their activities do homogenise open woodlands. This may contribute to the transformation of woodlands into grasslands.

Key Words: diversity, grasses, heterogeneity, saplings, seedlings, Tembe Elephant Park.

Introduction

Savannas are characterised by the coexistence of grasses and trees (Belsky 1990, Scholes & Archer 1997). Mechanisms sustaining this coexistence include the storage effect (Higgins *et al*. 2000), disturbance dynamics (van Langevelde *et al*. 2003) and localised heterogeneities (Jeltsch *et al*. 1998). The long-term existence of trees is vital for both the spatial (Jeltsch *et al*. 1998) and temporal (Higgins *et al*. 2000) models explaining this coexistence. Under certain conditions African elephants *Loxodonta africana* Blumenbach, can significantly increase the mortality rate of mature trees and potentially influence the coexistence of trees and grasses (Western & Maitumo 2004, Skarpe *et al*. 2004). Identifying the effect elephants may have for their environment is important for conservation management (Whyte *et al*. 2003) since disturbances such as fire, drought, trampling and herbivory can add to the impact of elephants on savannas (Ben-Shahar 1996, 1998, Dublin *et al*. 1990, Trollope *et al*. 1998).

Across African savannas, intact tree canopies provide microhabitats for shade tolerant plant species (Belsky & Canham 1994; Caylor *et al*. 2005). Shading by canopies reduces direct solar radiation and soil temperatures, and increase soil nutrients (Belsky *et al*. 1993; Ludwig *et al*. 2004) and water retention (Davis *et al*. 1998; but see Ludwig *et al*. 2004). Elephants may change these canopies by breaking branches and uprooting trees (e.g. Barnes 1982, Jachmann & Croes 1991, Lewis 1986). These changes may influence the species composition of the sub-canopy vegetation (Huntley 1991, Belsky & Canham 1994).

We examine how elephant-induced changes in the canopies of trees influence sub-canopy vegetation. Elephants are not the only agents that may influence some of the response variables. Other browsers and fire, may also affect plant species in the Park, but elephants dominate the browsing guild. We therefore often refer to the "park effect". We do however limit our study to tree species preferred by elephants and the associated community variables of grasses, woody seedlings and saplings. The study is based on the premise that intact tree canopies create microhabitats suitable for the establishment of shade tolerant grass and woody species. We hypothesised that the values will be smaller for community indices of grass, woody seedling and sapling assemblages associated with broken tree canopies than those associated with intact tree canopies.

Methods

Study area

The study area in northern KwaZulu-Natal, South Africa, includes the 300 km^2 Tembe Elephant Park (27°01'S 32°24'E) and some 200 km^2 of adjacent communal land (27°00'S 32°18'E) where few people live. Here the climate is sub-tropical with hot summers and cool to warm winters (Schulze 1982). From 1959 to 2002, the study area received a mean (±SD) annual precipitation of 748 ± 388 mm, as measured at the Park's head office. The landscape consists of undulating sand ridges with the highest point at 129m and the lowest at 50m a.s.l. (Matthews *et al*. 2001). Soil type and structure are similar both outside and inside the Park and are developed from relatively homogeneous, grey, siliceous, aeolian sands (Soil Classification Working Group 1991).

Recent elephant population estimates for the Park yield a crude density of 0.5 – 0.8 individuals per km^2 and a yearly rate of increase of 4.6 ± 0.06% (Morley 2005). The fencing of the Park, following its proclamation in 1983, excluded elephants from the adjacent communal land for 19 years before our study. The study site in the communal land experienced little resource extraction and no subsistence agriculture.

We focussed our study on the mixed woodlands. Broadleaved trees such as *Terminalia sericea* Burch. Ex DC, *Euclea natalensis* A.D.C., *Strychnos spinosa* Lam., *S. madagascariensis* Poir, *Combretum molle* R.Br. ex G.Don and *Afzelia quanzensis* Welw. are prevalent in these mixed woodlands. Based on tree and shrub density we divided the mixed woodlands into closed (mean ± SE distance between trees higher than 4m = 13 ± 0.2 m) and open woodland types (21 ± 0.4 m). The closed woodland consists of dense stands of shrubs and undergrowth with a closed and layered canopy. A grass layer and sparsely spaced mature trees dominate the open woodland. Fire is prevalent both inside and outside the Park. Park management opts for scheduled burning at the end of the dry season while fires outside the Park may occur year round. The sampling sites selected for the present study did not burn before or during the study but the fire history of the sampling sites is unknown.

Experimental design

We followed a stratified random sampling design (Krebs 1999). We distinguished between a trial area inside the Park where elephants live and a control area within the communal land where no elephants occur and where few people live. Strata were based on the two woodland types. Sampling was conducted from January to May 2002 at 19 sites, with nine sites in the closed woodland (five sites inside and four sites outside the Park) and ten sites in the open woodland (five sites both inside and outside the Park). We selected sites based on a classified satellite image for the Park and its immediate surroundings (Harris, van Aarde & Pimm, unpublished data, using a cloud free partial scene ID 167-79 of 30 August 1999). Our visit to sites outside the Park confirmed no human and/ or signs of livestock present at the selected sites.

A single line transect was randomly placed at each site, the length of which varied between two to five kilometres depending on the distance between the sampled trees. We generated random numbers (between 10 and 20) with a spreadsheet, to select the fifteen mature trees (tree samples) with a maximum canopy height > 4 meters along each transect. Selected trees were chosen from amongst the group of 15 species that were high in elephant dietary preference within Maputaland (de Boer *et al*. 2000, Klingelhoefer 1987; Appendix 3.1). Each tree was visually assessed and assigned to one of five classes depending on percentage canopy removed by elephants (1 = < 10%, 2 = 10–24%, 3 = 25–74%, 4 = 75–99%, and 5 = canopy entirely removed). Four sub-samples (using a one m^{-2} sample grid) were located at a distance of two meters from the main stem(s) of the sampled tree in the four orthogonal compass directions. Live standing woody elements within each of these were identified, separated into seedling (< 0.5 m) and sapling (0.5–2 m) classes and counted. Grasses were identified and cover-abundance values (adapted from Werger 1974) assigned as; 1 = single individual, 2 = present with < 1% cover, 3 = numerous and cover 1–5%, 4 = very numerous and cover 1–5%, 5 = cover 5–12%, 6 = cover 13–25%, 7 = cover 26–50%, 8 = cover 51–75%, 9 = cover 75–99%, 10 = single species dominance. Another four sub-sample quadrats were placed at a distance of 20 m from the sampled tree stems, perpendicular to the line transect and the sampling of grasses, woody seedlings and saplings were repeated at these locations. These served as local controls to each tree sample and represent woodland specific characteristics (shaped by ecological events other than elephants alone i.e. different fire regimes, the presence or absence of herbivory, etc.) both inside and outside the Park.

Data analysis

Elephant impact on the canopies of pre-selected trees was determined using a one-tailed G-test (Sokal & Rohlf 1995) that tested for differences in the frequency distribution of trees in canopy removal classes inside and outside the Park. Abundance values for grasses, woody seedlings and saplings were totalled separately over the four sub-samples for each tree and the associated local control. We calculated Margalef's (d) index for species richness, the reciprocal of Simpson's (λ) for diversity and the Pielou's evenness (J') as an evenness index, using PRIMER-E statistical software (Clarke & Warwick 2001). We 4th-root transformed indices values (Clarke & Warwick 2001). We used a 2 X 2 factorial analysis of variance (Sokal & Rohlf 1995) to test for significant differences between inside/ outside the Park and tree samples/ local controls for each woodland type.

Results

There were significantly more trees within the higher reduced canopy classes inside than outside the Park (closed woodland: $G = 114.4$, $df = 4$, $P < 0.0001$; open woodland: $G = 122.8$, $df = 4$, $P < 0.0001$; Fig. 3.1). This was especially the case in the open woodlands where more tree canopies were damaged than in the closed woodlands. In open woodlands almost 50% of the sampled trees had more than half of their canopies removed. Less than 10% of the trees sampled within the closed woodlands lost most of their canopies (Fig. 3.1).

Within closed woodlands, we found no significant interaction between factors (the Park and tree canopies) for indices of the sub-canopy plant assemblages (Table 3.1, Fig. 3.2). For some indices the canopy and Park effects differed. For instance, underneath tree canopies, all indices for grass assemblages were significantly lower than those for the local controls. However, for sapling and seedling assemblages these indices were higher (apart from seedling evenness) than those for the local controls. Inside the Park, indices for grasses were higher than outside the Park, while those for saplings were lower inside the Park than outside. For seedlings, there were no significant differences in the indices inside and outside the Park (Table 3.1, Fig. 3.2).

The situation within the open woodlands differed from those in the closed woodlands. For instance, for the grass and sapling indices we recorded a significant interaction between factors (the Park and tree canopies). This was not the case for the seedlings indices (Table 3.1, Fig. 3.2). Grass species richness and evenness were lower, but diversity higher underneath tree canopies than local controls. All seedling and sapling (except for sapling diversity) indices underneath tree canopies were significantly higher than local controls. Inside the Park, all grass indices were higher, but sapling indices were lower than outside the Park.

Discussion

We aimed to identify the influence of elephants for vegetation in an African savanna. To achieve this we searched for changes in sub-canopy vegetation with changes in canopy shapes induced by elephants. We distinguished between open and closed woodlands as differences in their structures and tree densities may influence the response of sub-canopy vegetation to disturbances. At our study site, like elsewhere, elephants changed tree canopies (Barnes 1982, Jachmann & Croes 1991, Lewis 1986), thereby affecting the microhabitat (Belsky *et al.* 1993, Belsky & Canham 1994). We compared sub-canopy community variables of areas exposed to elephants (inside the Tembe Elephant Park) with those of areas protected from elephants (local communal lands adjoining the Park). We recognised that browsers and grazers other than

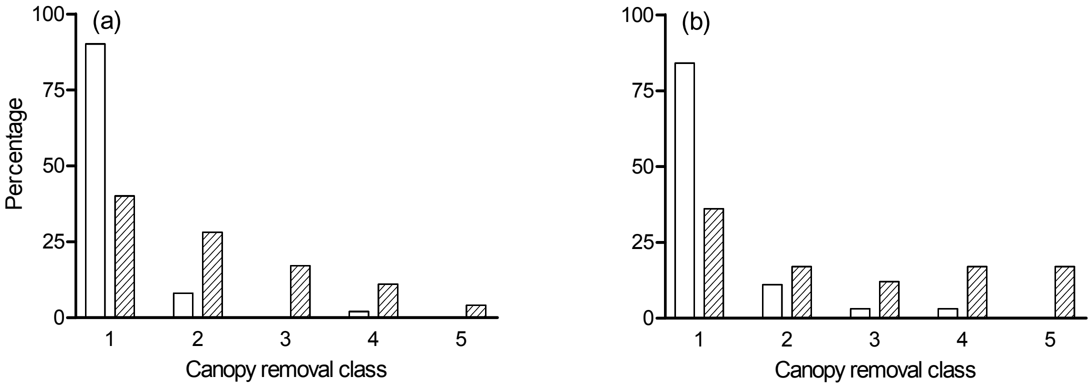

Figure 3.1. Frequency distributions of percentage of sampled trees within each canopy removal class for (a) the closed and (b) open woodland outside (clear bars) and inside (diagonal lines) the Tembe Elephant Park.

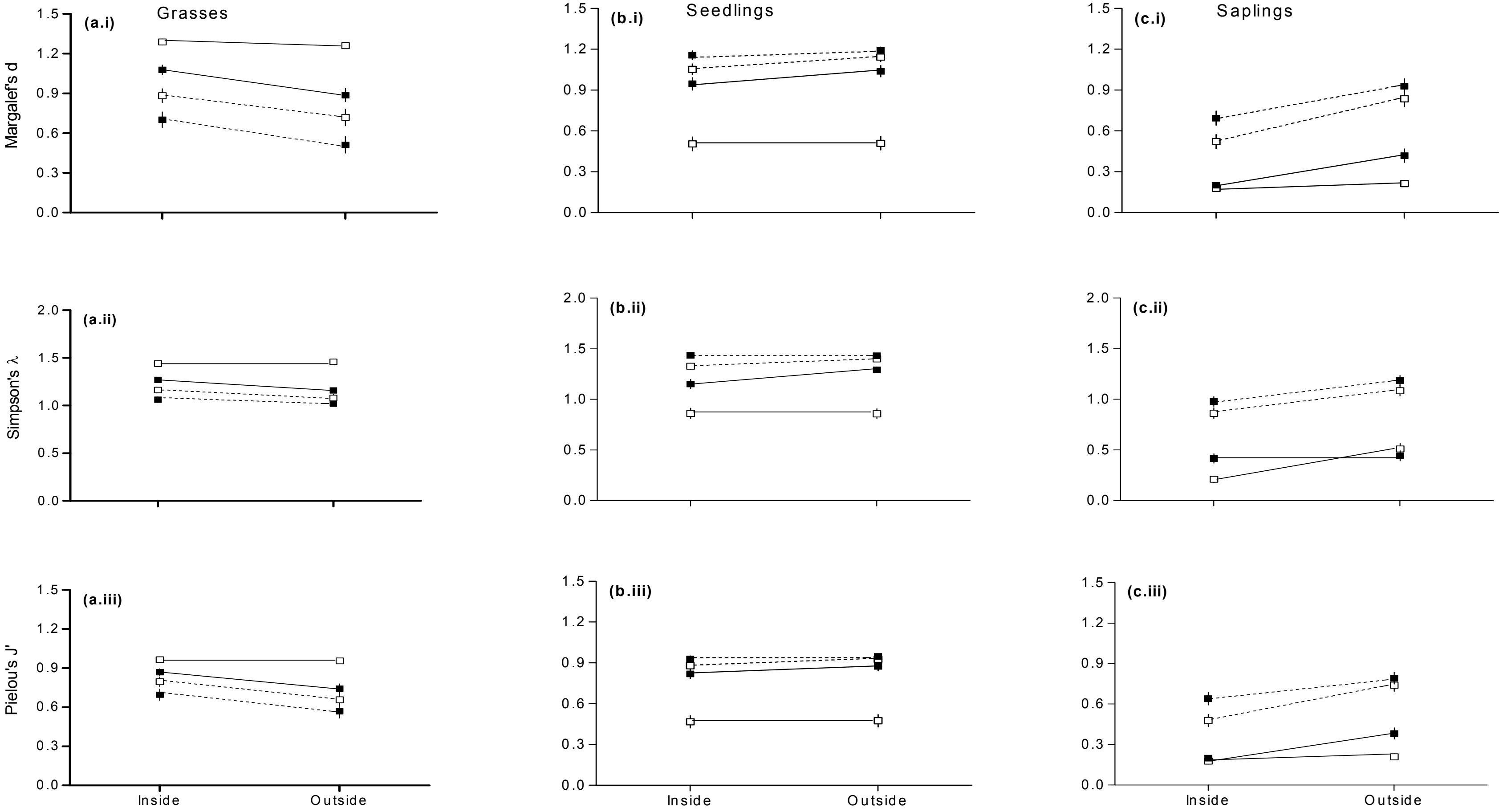

Figure 3.2. Mean (±SE) species richness (i), diversity (ii) and evenness (iii) for grasses (a), woody seedlings (b) and saplings (c) within the closed (dotted lines) and open woodlands (solid lines) inside and outside the Tembe Elephant Park. The solid squares represent tree samples and the open squares the local controls.

Table 3.1. F–values using a 2X2 factorial ANOVA for grass, woody seedling and sapling indices within the closed (n = 135) and open woodlands (n = 150). Canopy represents the difference between the sampled tree and the associated local control, Park denote differences between inside and outside the Park and Canopy*Park reflect on the interaction between the two factors. Arrows indicate direction of change from the sampled tree to the associated control, and inside to outside the Park. (P < 0.05*, P < 0.01**, P < 0.001***, NS non-significant).

		Closed woodland			Open woodland		
		Richness	Diversity	Evenness	Richness	Diversity	Evenness
Grass	Canopy	↓ 10.88**	↓ 7.92**	↓ 4.51*	↓ 75.03***	↑ 142.56***	↓ 43.53***
	Park	↑ 9.06*	↑ 4.90*	↑ 8.87**	↑ 10.45**	↑ 5.26*	↑ 8.31**
	Canopy*Park	NS	NS	NS	5.73*	10.72**	6.14*
Seedlings	Canopy	↑ 5.12*	↑ 6.90**	NS	↑ 106.02***	↑ 65.43***	↑ 89.19***
	Park	NS	NS	NS	NS	NS	NS
	Canopy*Park	NS	NS	NS	NS	NS	NS
Saplings	Canopy	↑ 5.76*	↑ 4.27*	↑ 5.17*	↑ 17.32***	NS	↑ 16.76***
	Park	↓ 25.16***	↓ 17.03***	↓ 19.73***	↓ 21.23***	↓ 13.34***	↓ 20.76***
	Canopy*Park	NS	NS	NS	11.06***	9.44*	10.14**

elephants living inside the Park may influence the responses we recorded. These responses thus may be considered as a "park effect" rather than an "elephant effect".

Nearly 60% of the trees in closed and open woodlands inside the Park had altered canopies, whereas the canopies of most trees (80%) on communal lands were intact. The altered canopies outside the Park may be ascribed to natural tree mortality, or remnants of elephant browsing before the Park were fenced. Independent of canopy shape and woodland type indices for grasses were lower at trees than at controls. The opposite was true for seedlings and saplings. In open woodlands, trees within intact canopies were associated with more seedlings and saplings than control sites. Here the perennial grass species *Panicum maximum* Jacq. dominated while controlled sites supported a variety of pioneer grass species (Ludwig *et al*. 2004).

Grass and woody sub-canopy species in closed woodlands did not respond to the small changes (<10% totally removed) in tree canopies. As elsewhere, (e.g. Favier *et al*. 2004) gaps that developed in response to elephant feeding in closed woodlands may favour grass growth (Norton-Griffiths 1979). This could result from variability and increase in sunlight (Naumburg & de Wald 1999; Ludwig *et al*. 2004).

The relatively low community indices for saplings inside the Tembe elephant Park may not only be ascribed to elephants, but also to browsing by species such as kudu *Tragelaphus strepsiceros* Pallas, nyala *Tragelaphus angasii* Gray, impala *Aepyceros melampus* Lichtenstein, red duiker *Cephalophus natalensis* A. Smith and suni *Neotragus moschatus* von Dueben). The decrease in the sapling evenness may be result from selective browsing that reduces dominant species (exploiter-mediated coexistence; Begon, Harper & Townsend 1996). Furthermore, elephants may have facilitated (*sensu* Connell & Slatyer 1977; van de Koppel & Prins 1998) the growth of saplings by reducing the inhibitory effect of shading by canopies. This may also hold for open woodlands.

In the open woodlands of Tembe, elephants reduced tree canopies. This and frequent hot fires may have reduced the grasses and woody saplings. Fire is unselective (Bond *et al*. 2005) and may reduced dominant grasses, thus explaining inducing increased species richness and evenness (see Pimm 1991). This and changes in tree canopies may have generated similar recruitment and establishment conditions for grasses at both our treatment and control sites. Grasses accordingly increased in diversity and evenness. Browsing and fire may keep woody elements within the flame zone, and stop saplings from further development. This situation may be similar to the fire-mediated recruitment bottleneck referred to by Higgins *et al.* (2000).

In our study area seedlings, on the other hand, were not influenced by canopy changes. This differs from other studies (e.g. Barnes 2001; Jachmann & Croes 1991) where elephants destroy seedlings. Canopies may provide microhabitat conditions for the establishment of seedlings (e.g. through establishing fertility patches; Anderson *et al*. 2001), but changes in the canopy clearly have little consequence for seedlings once they have been established (see Caylor *et al*. 2005).

To summarise, our study suggests that elephants enhance the structural heterogeneity of closed woodlands but homogenise that of woodlands. This is supported by the significant interactive term between the overall "park effect" and reduced canopy structures for grass and saplings indices in the open woodland (see Table 3.1). Inside the Park, there is a higher similarity in the respective grass and saplings indices between tree samples (with their canopies modified by elephants) and their local controls.

The coexistence of trees and grass in African savannas rely on the long-term survival of trees (e.g. Higgins *et al.* 2000, Jeltsch *et al.* 1998, van Langevelde *et al*. 2003). Elephants can remove trees or change their canopies and therefore affect tree/ grass ratios. With this and the interactive effects of herbivory and fire (Dublin *et al*. 1990) may result in a gradual shift from a mosaic of closed and open woodland types to an open grassland state.

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Appendix 3.1

Tree species (listed alphabetically) selected for this study are based on those most preferred by elephants in the Maputaland region (extracted from de Boer *et al.* 2000 and Klingelhoefer 1987). Species names follow Arnold & de Wet (1993).

Species name	Common name
Acacia burkei Benth.	Black Monkey Thorn
Acacia karroo Hayne	Sweet Thorn
Afzelia quanzensis Welw.	Pod Mahogany
Albizia adianthifolia (Schumach.) W.F.Wight	Flat-crown
Albizia versicolor Welw. ex Oliv.	Large-leaved False-thorn
Combretum molle R. Br. ex G. Don	Velvet Bushwillow
Dialium schlechteri Harms	Sherbet Tree
Garcinia livingstonei T.Anders	African Mangosteen
Manilkara discolor (Sond.) J.H. Hemsl.	Forest Milkberry
Sapium integerrimum (Hochst.) J. Leonard	Duikerberry
Sclerocarya birrea (A.Rich.) Hochst.	Marula
Spirostachys africana Sond.	Tamboti
Strychnos madagascariensis Poir.	Black Monkey Orange
Terminalia sericea Burch. ex DC.	Silver Cluster-leaf
Trichilia emetica Vahl.	Natal Mahogany

Chapter 4

Manuscript prepared for submission to the Journal of Ecology

The impact of elephants on plant community variables of the Tembe Elephant Park

Robert A.R. Guldemond & Rudi J. van Aarde

Summary

1 Elephants confined to protected areas may affect local biological diversity. We expect measurable deviations in woody plant community variables such as density, species composition, abundance-incidence and rank-abundance patterns when exposed to elephant browsing.

2 We examined these plant community variables in the presence and absence of elephants for both mixed woodlands (closed and open woodland types) and sand forests inside Tembe Elephant Park and adjacent communal land in South Africa.

3 Mixed woodlands and sand forest species composition differed significantly between the Park and the communal land. Woody plant densities, abundance-incidence and rank-abundance relationships inside the Park were not, however, significantly different from those recorded in communal land.

4 Regional and local ecological processes such as plant metapopulation dynamics, niche partitioning and other disturbance events (*e.g.* frequent fires) may mask the localised impact elephants have for rare woody plant species in the Park.

Key-words: abundance, composition, density, incidence, species rank, woodlands

Introduction

Ecological assemblages typically comprise of few dominant species and a large number of relatively rare species (Sugihara 1980; Tokeshi 1993; Gaston 1994; Lennon *et al*. 2004). A number of models predict these rank abundance patterns (e.g. Magurran & Henderson 2003; Ulrich & Ollik 2004). Further, plant and animal assemblages across a wide range of spatial and temporal scales (Guo *et al*. 2000) and disturbance regimes (Gaston & Warren 1997) are characterised by positive abundance incidence relations (Hanski 1982; Brown 1984; Gotelli & Simberloff 1987; Collins & Glenn 1990; Maurer 1990; Hanski & Gyllenberg 1993; but see Gaston & Lawton 1990; Gaston 1996). This may be explained by plant meta-population dynamics (Hanski & Gyllenberg 1993; van Rensburg *et al*. 2000), niche-breadth / resource partitioning (Brown 1984; Guo *et al*. 2000) and the related resource availability hypothesis (Gaston 1994; Hanski *et al*. 1993). Recently, neutral models suggest an alternative explanation for relative species abundance distributions (Hubbell 2001; Volkov *et al*. 2003; but see McGill 2003; Gilbert & Lechowicz 2004; Magurran 2005).

Savanna elephants (*Loxodonta africana*) influence biological diversity especially when confined and occurring at relatively high densities (Laws 1970; Cumming *et al*. 1997; Western & Maitumo 2004; but see Wiseman *et al*. 2004). Under such conditions, their foraging and feeding habits may reduce tree densities and transform forests and intact woodlands into mixed woodlands and even grasslands (e.g. Dublin *et al*. 1990; Lock 1993; Barnes *et al*. 1994; Leuthold 1996; Ben-Shahar 1998; Trollope *et al*. 1998; van de Vijver *et al*. 1999; Eckhardt *et al*. 2000; Mosugelo *et al*. 2002). Such conversion may be associated with changes in the abundance-incidence and rank-abundance functions that described woody plant communities. An investigation into these relationships in areas exposed to elephant browsing then may illustrate how disturbance may affect these community variables.

The Tembe Elephant Park in the Maputaland centre of plant endemism (van Wyk 1996) represents a case of confined elephants occurring at relatively high densities. In addition to elephants, the Park protects a unique sand forest ecotype that supports several endemic plant species (van Wyk 1996). Elephants may negatively affect these unique sand forest elements (Matthews *et al*. 2001; van Rensburg *et al*. 1999) and like elsewhere this may call for management operations such as elephant culling (e.g. van Aarde *et al*. 1999; Whyte *et al*. 2003) or the application of contraceptives (Pimm & van Aarde 2001).

The present study investigates the consequences of elephant presence for the abundance-incidence and relative rank-abundance relationships of woody plants in Tembe Elephant Park. Other herbivores also occur in the Park, and therefore, for this study, the presence of elephants describes a “park effect”. The surrounding study area has few herbivores, no elephants and hardly any people living there. This allows us to use the comparative method to determine if elephants, along with other browsers, modify the abundance-incidence and rank-abundance relationships for woody species. We expected a reduction in the abundance of woody species when exposed to these animals, which through selection for certain species could change the slope and intercepts of the lines describing the abundance-incidence and rank-abundance relationships.

Materials & Methods

The study area

The study was conducted in Tembe Elephant Park (27°01'S 32°24'E) (300 km^2) and adjacent communal land (200 km^2) situated within the Maputaland region of northern KwaZulu-Natal, South Africa. Elephants always occurred in Maputaland, but have been confined to the Park since 1989 following the fencing of its northern boundary, which borders southern Mozambique. During 2001 an estimated 179 elephants (95% CI of 136 to 233) resided in the Park, and the population is presently increasing at a rate of 4.64±0.06% per annum (Morley 2005).

From 1959/60 until 2001/02 (corrected for the June-July rainfall season) the area received a mean (±SD) annual rainfall of 748±388 mm. Sand forests and mixed woodlands dominate the landscape (Matthews *et al.* 2001). Van Wyk (1996) describes sand forests as a very dense and dry semi-deciduous to deciduous forest type. Based on tree and shrub densities, we divided the mixed woodlands into closed and open woodland types (adapted from Edwards 1983; One-tailed t-test t_{257}=13.45, P<0.0001). Dense stands (mean ± SD; 2,423.3±873.1 / ha^{-1}) of trees, shrubs and undergrowth, with an enclosed and layered canopy cover characterise the closed woodland. Grass swards and sparsely spaced mature trees and shrubs (1,060.9±728.9 / ha^{-1}) dominate the open woodland.

Experimental design

We considered the absence of elephants in communal land outside the Park and on its fringes as a regional control, and elephant presence inside the Park as the trial. We selected sites based on a classified satellite image for the Park and surroundings

(Harris, van Aarde & Pimm, unpublished data, using a cloud free partial scene ID 167-79 of 30 August 1999). Our visit to sites outside the Park confirmed no human and/ or livestock at the selected sites. Our follow-up visit to these sample sites in the communal land confirmed low human habitation, no subsistence farming and limited resource extraction.

The design follows a stratified random sampling procedure (Krebs 1999), with strata based on the woodland types (sand forests, closed and open woodlands). We selected three sampling sites inside and three outside the Park for each woodland type and randomly placed 16X16m quadrats within each site (Kent & Coker 1992). The number of quadrats per woodland type varied and range from 60 for the sand forests, 120 in the open and 139 in the closed woodlands. We identified, enumerated and documented all trees and shrubs standing higher than 0·5m within each quadrat.

Data analysis

We expressed tree and shrub densities as the total number of individuals enumerated within each quadrate, and analysis of variance (ANOVA) (Sokal & Rohlf 1995) to test for significant difference in densities between inside and outside the Park. We investigated differences in species composition for each woodland type between inside and outside the Park using a Bray-Curtis similarity coefficient in an analysis of similarity (ANOSIM) with the PRIMER-E software package (Clarke & Warwick 2001). Mean abundance values for each species were only calculated from quadrats in which the species occurred (Wright 1991; Gaston 1996). These were $\log_{10}$-transformed before analysis due to non-normality in species abundance distributions (Sokal & Rohlf 1995). Due to uneven number of quadrats (between 10 and 25) for each of the sampling sites, incidence is expressed as the proportional number of quadrats in which each species occurred. We used least square regression analysis (Blackburn & Gaston 1998) to quantify the relationship between woody species abundance and incidence, and ANOVA to test for significant differences between the slopes of the relationships inside and outside the Park. Rank-abundance curves were constructed (Krebs 1999) and a Kolmogorov-Smirnov two-sample test (Tokeshi 1993) used to statistically compare abundance values for the woody species inside and outside the Park. We used the geometric-series models to compare plant community patterns between the three woodland types (Tokeshi 1993).

Results

Tree and shrub densities inside and outside the Park were similar for the three woodland types ($F_{1,313}$=0.26, P=0.61). Based on an ANOSIM, species composition inside and outside the Park, however, differed significantly from each other for all woodland types (sand forest: Global R=0.24, P<0.001; closed woodland: Global R=0.25, P<0.001; open woodland: Global R=0.11, P<0.001). Expressing abundance as a function of incidence yielded a positive relationship for all the woodland types inside and outside the Park (Table 4.1). Only a small amount of the variation in abundances, however, could be explained by incidence, especially for the closed and open woodlands (Table 4.1).

The slopes of the relationships (sand forest: $F_{1,98}$=0.56, P=0.46; closed woodland: $F_{1,212}$=1.21, P=0.27; open woodland: $F_{1,120}$=0.63, P=0.43) for trees and shrubs were similar, as were the intercept values for assemblages inside and outside the Park (sand forest: $F_{1,99}$=3.54, P=0.06; closed woodland: $F_{1,213}$=0.09, P=0.76; open woodland: $F_{1,121}$=0.01, P=0.93) (Fig. 4.1).

Table 4.1 Regression statistics for abundance-incidence relationships for woody species inside and outside the Park indicating significant deviation from zero for the respective woodland types. However, no significant difference was found in the slopes of the relationships inside and outside the Park (for the sand forest: $F_{1,98}$=0.56, P=0.46; closed woodland: $F_{1,212}$=1.21, P=0.27 and open woodland: $F_{1,120}$=0.63, P=0.43 respectively; refer Fig. 4.1).

	Sand forest		Closed woodland		Open woodland	
	Inside	Outside	Inside	Outside	Inside	Outside
Deviation	$F_{1,58}$=58.68***	$F_{1,40}$=58.30***	$F_{1,99}$=16.20***	$F_{1,113}$=35.73***	$F_{1,58}$=4.182*	$F_{1,58}$=13.37***
Intercept	1.09±0.04	1.04±0.04	1.17±0.03	1.15±0.03	1.19±0.03	1.17±0.03
Slope	0.78±0.10	0.67±0.09	0.44±0.11	0.60±0.10	0.32±0.16	0.48±0.13
r^2	0.50	0.59	0.14	0.24	0.06	0.19

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

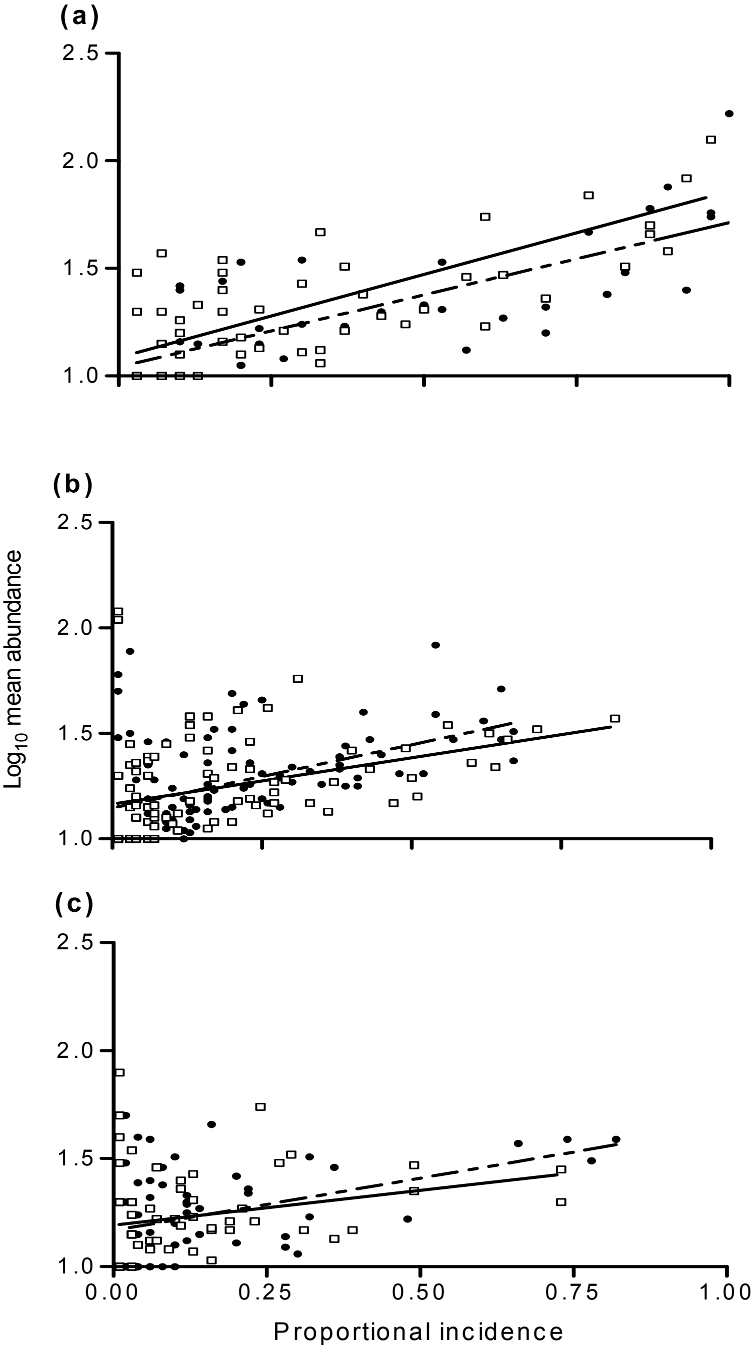

Fig. 4.1 Log$_{10}$ mean abundance as a function of the proportional incidence for a) sand forests, b) closed woodland and c) open woodland for trees and shrubs inside (open squares & solid lines) and outside (solid circles & dashed lines) the Tembe Elephant Park.

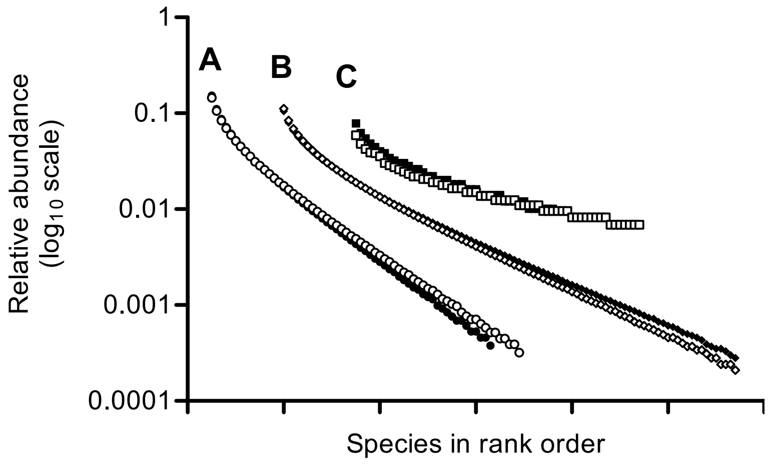

Fig. 4.2 The relative abundance ranked for trees and shrubs in the (A) open woodland, (B) closed woodland and (C) sand forests inside (open) and outside (solid) Tembe Elephant Park.

Likewise, species-specific abundance did not differ significantly inside and outside the Park (Kolmogorov-Smirnov test (α=0.01) for sand forest: D_α=2.298 n=60; closed woodland: D_α=2.304, n=114; open woodland: D_α=2.302, n=65; Fig. 2). The geometric-series models indicated a significant change in the species abundance pattern between the three woodland types ($F_{5,429}$=20.26, P<0.0001). These differences appear to be independent of elephant presence, with the open woodland having the steepest slope, then the closed woodland, with most evenly spread species abundance in sand forests (Fig. 4.2).

Discussion

Consequences of the feeding and foraging behaviour of confined elephant populations are important for woody species, especially when developing conservation management options (e.g. Whyte *et al*. 1999, 2003). The present study aimed at identifying the impact of a disturbance brought about by elephants and other herbivores for selective plant assemblage characteristics. The Park supports a suite of browsers other than elephants, none of who also occur outside the Park. However, elephants dominate the mammalian browser guild and most of the impact noted may therefore be ascribed to elephant browsing *per se*. Fire too can suppress woody seedlings and saplings from attaining maturity (Higgins *et al*. 2000); and we therefore refer to the apparent impact recorded through our comparative approach as the "park effect" rather than the elephant effect.

The scatter of the data points around the abundance-incidence regression line, especially within the closed and open woodlands, displays the typical curvilinear and triangularity encountered in numerous other studies (for summary see Gaston 1994). Low correlation values for plant species may be due to plant species either having a high biomass but low densities and/ or high biomass due to small individual size and high numbers (see Hanski *et al.* 1993). For all three woodland types inside and outside the Park, we recorded positive and similar relationships in the abundance-incidence relationships for trees and shrubs. Plant species abundance was, therefore, unaffected by the "park effect". Similarly, Gaston & Warren (1997) showed that under controlled laboratory experiments disturbance does not affect the slopes, intercepts, or coefficients of determination of the interspecific abundance-distribution relationships. Our findings, under more natural conditions in the Tembe Elephant Park, suggest that the abundance-incidence relationships of woodland species were resistant to elephant-induced changes. More importantly, the interspecific positive abundance-incidence relationships defined over a wide range of spatial and temporal scales (Guo *et al.* 2000), assemblages and disturbance regimes (Gaston & Warren 1997), may be assigned as one of the general rules in ecology (Hanski *et al.* 1993; but see Gaston & Lawton 1990). Elephants, along with the other herbivores, may therefore be unable to alter the abundance-incidence for woody plant species.

The plant community structure, as reflected in the rank-abundance pattern, shows typical dominance in abundance of a few common species, with most species only represented by a few individuals (Gaston 1994). The "park effect" on trees and shrubs seem to have little consequence for this pattern. The plant community structures for the three woodland types, that is the presence of mostly rare species with a few dominant species, remain intact in the presence of elephants. The slopes describing rank-abundance, however, differed significantly between the landscape types, both inside and outside the Park. The steepness of the slopes was higher for the sand forest than those for the closed and open woodlands. This suggests that the latter woodland type could represent an early successional stage of the more complex closed woodland or sand forest type; Tokeshi (1993) gives a similar scenario. On the other hand, frequent fires may prevent open woodlands from developing into closed woodlands (see Higgins *et al*. 2000).

Both regional and local ecological processes could still mask the potential impact of especially, elephants on trees and shrubs in Tembe Elephant Park. These processes may include other disturbance events (e.g. fire), meta-population dynamics (Hanski & Gyllenberg 1993, van Rensburg *et al*. 2000) and resource partitioning / niche-based models (Brown 1984; Guo *et al*. 2000), which are currently believed to structure ecological communities (Gaston *et al*. 1997). The rank-abundance patterns we found also suggest that at current densities elephants have no impact on the rare species within the Park and that the plant community structure remain intact. This is particularly important for the conservation of the rare and endemic sand forest species. We conclude that elephants in Tembe Elephant Park, under current densities, do not change the slopes and intercepts of the lines describing the abundance-incidence and rank-abundance relationships, despite the differences in species compositions between inside and outside the Park.

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Chapter 5

Manuscript prepared for submission to the Journal of African Ecology

Range constriction and landscape use of elephants in Maputaland, southern Africa

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Abstract

We investigated the effects of confinement for spatial and landscape use by elephants in Maputaland. We constructed 95% minimum convex polygons home range areas and used compositional analysis to determine landscape selection. Elephants in southern Mozambique roam freely while those in Tembe Elephant Park are confined. Free-ranging individuals had larger home ranges than those confined by fences. Free-ranging elephants show preference for closed woodlands. Confined elephants show no clear landscape selection, besides avoiding reed beds during the dry season. Home range sizes of elephants in Tembe Elephant Park are not significantly smaller than those predicted by rainfall, based on elephants studied across southern Africa. However, confined elephants have smaller home ranges than free ranging ones. At the same time, providing artificial water may change landscape selection patterns. Park management should reconsider reinstating elephant space use by removing fences and artificial water.

Keywords: artificial water, fences, Maputo Elephant Reserve, rainfall, reed beds, sand forests, Tembe Elephant Park, woodlands.

Introduction

African elephants are generalists and occupy landscapes ranging from semi-deserts to forests (see Blanc *et al.*, 2003). Local space use patterns also vary (e.g. Douglas-Hamilton, 1973; Viljoen, 1989). Factors including rainfall (Leuthold & Sale, 1973; Western & Lindsay, 1984; Thouless, 1996; Verlinden & Gavor, 1998), resource distribution (Jachmann, 1983; Osborn, 2003), social interactions (de Villiers & Kok, 1991; Wittemeyer, Douglas-Hamilton & Getz, 2005; Charif *et al.*, 2005), site-specific differences in the behaviours of bulls and breeding herds (Leuthold & Sale, 1973; Viljoen, 1989) and landscape heterogeneity (Grainger, van Aarde & Whyte, in press) may all influence landscape use. Artificial disturbances such as human induced compression of elephants into "disturbance free-space" (Lamprey *et al.*, 1967; Western & Lindsay, 1984), illegal activities (Jachmann, 1983; Western & Lindsay, 1984) and culling (van Aarde, Whyte & Pimm, 1999) may further influence local space and landscape use.

The development of conservation areas across the distributional range of elephants often limits them to fenced areas. Relatively high human densities around unfenced conservation areas may also restrict movements (Hoare, 1999; Hoare & du Toit, 1999; O'Connell-Rodwell *et al.*, 2000). Such restrictions may reduce home ranges, and could thereby intensify the impact that elephants have on vegetation. Few opportunities exist to test this generalisation. Free-ranging and confined elephants living in Maputaland, however, provide for such an opportunity.

Maputaland's elephant population was recently fragmented into two sub-populations. Here, elephants in Tembe Elephant Park are fenced into an area covering 300 km^2. Other elephants in the region roam freely across an area of about 1500 km^2 within Maputo Elephant Reserve and the Futi River Corridor in southern

Mozambique. In this study, we compare home ranges for neighbouring elephants living under these contrasting conditions, but in the same landscapes. We relate our observations to published and unpublished records for elephants across southern Africa. We test the hypothesis that rainfall, rather than constriction explains variation in home range area in elephants. Should confinement influence ranging behaviour we expect that the home ranges of confined elephants to differ from those of free-ranging elephants exposed to similar rainfall conditions.

Materials and methods

The study site

The Tembe Elephant Park (TEP) (27º01'S 32º24'E) is situated in the northern KwaZulu-Natal Province (South Africa) and Maputo Elephant Reserve (MER) (26°25'S, 32°45'E) and Futi River Corridor (FC) in southern Mozambique. Geographically, the FC (~700km^2) connects the TEP (300km^2) and MER (800 km^2) and is now protected by limiting the number of people living here (Soto, Munthali & Breen, 2002). Elephants move freely through the unfenced MER and FC. An electrified elephant-proof fence, situated along the international border between South Africa and Mozambique, separates TEP from FC and MER (Sandwith, 1997). Some 204 elephants live in southern Mozambique, while 179 are presently confined to the TEP (Morley, 2005).

Mean (±SD) annual rainfall, from July to June for southern Mozambique (measured at Changalane from 1980 to 2002) is 757 ± 226 mm. This is similar to the 718 ± 371 mm recorded for TEP (measured at Sihangwane from 1959 to 2002). The cumulative surplus/deficit trends in rainfall (Dunham, Robertson & Grant, 2004) and the duration of the wet and dry seasons are also similar across these areas (Figs. 5.1a

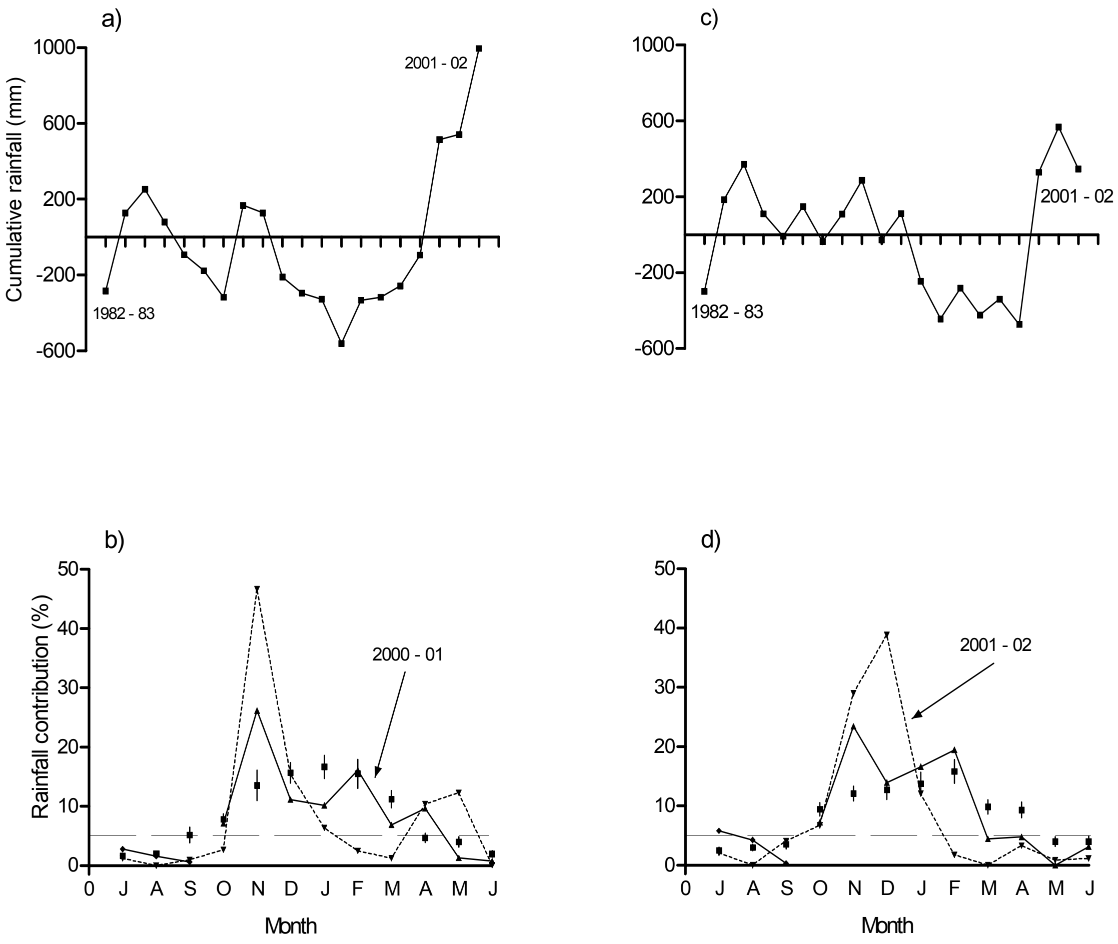

Figure 5.1. The MER & FC (a) and TEP (c) received higher than average rainfall during the study period as shown by the cumulative deficit/surplus rainfall patterns for the respective areas. We define dry seasons by the months contributing less than 5 % of the annual total for (b) MER & FC and (d) TEP. The solid (2000–01) and dotted (2001–02) lines track the monthly rainfall for the study duration. The square blocks and lines indicate the mean (± SE) percentage rainfall typical for each month and the horizontal dashed line indicate the 5% cut-off percentage in monthly rainfall contribution defining the wet and dry seasons (see text for details).

& c). We define wet and dry based on the percentage contribution of monthly rainfall to the mean annual rainfall. Each dry season month contributed less than 5 % to the annual rainfall. Subsequently, we deemed May to September as the dry season months, while the wet season months of October to April accounted for > 80 % of the annual rainfall (Figs. 5.1b & d).

A supervised vegetation classification using ERDAS IMAGINE 8.7 software (Leica Geosystems GIS & Mapping LLC, Illinois) of Maputaland provided information on the dominant landscape types for the study area (Harris *et al.* in review, using a cloud free partial scene ID 167-79 of 30 August 1999[*]). We grouped landscapes into forests (combining sand, swamp and coastal dune forests), closed woodlands, open woodlands and reed beds (Kappa statistic = 80%). The relative sizes of the landscapes between southern Mozambique and TEP are similar with forests contributing 31% vs. 33%, closed woodlands 37% vs. 44%, open woodlands 30% vs. 23% and reed beds 3% vs. < 1% respectively.

Sampling design

The study period from October 2000 to September 2002 provided information on the locations of elephants that roamed across the area for two wet and dry seasons. Here nine elephants were fitted with satellite collars (ST–14 Platform Transmitters Terminal, Telonics, Arizona, USA). These included one bull and three cows in TEP and three bulls and two cows in southern Mozambique. The collar on the bull in TEP failed after one year, and one of the bulls collared in southern Mozambique did not record information during the 2002 (second) dry season. All transmitters were active

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[*] "In all sites, we took GPS points demarcating vegetation and vegetation transitions. Many of these points trained our signatures for vegetation mapping, using supervised classification techniques with maximum likelihood decision rules. Each vegetation map was smoothed with a 3X3 majority filter to remove pixel scatter, and received validation via a kappa statistic" (from Harris *et al.* in review).

for 24 hours and inactive for 48 hours thereby providing at least one location each third day. Location accuracy ranged from 0–350m (class 2 & 3 accuracy; Argos, 2000). The number of locations of each elephant for each season are summarised in Table 5.1.

We used computerised databases, the African Elephant Bibliography (http://www.elephant.chebucto.net) and hand searches through references lists (cited in this chapter's reference list) to find studies with home range estimates for elephants bounded between the 10º and 28º latitudes south of the equator. We excluded data for forest elephants (*Loxodonta cyclotis* Matchie, 1900) and those occurring in the hybrid zone delineated by Roca, Georgiades & O'Brien (2004). Data on elephant locations currently collected by CERU across southern Africa, supplemented the information of the collated studies (Jackson & Erasmus, unpublished report). We also documented rainfall and whether elephants' movements were constrained by fences and/ or through the provision of artificial waterholes.

Data analyses

We calculated seasonal home ranges for each elephant as the 95 % minimum convex polygon (MCP; see White & Garrott, 1990) using Ranges 6 v1.2 software (Kenward, South & Walls, 2003). The number of locations per individual may influence estimates of the home ranges (Girard *et al*., 2002) and we tested for stabilisation of these with incremental analysis (Kenward *et al*., 2003).

Spatial and temporal autocorrelation (Swihart & Slade, 1985) may bias the interpretation of elephant home range and landscape preference. Autocorrelation is analogous to pseudoreplication, which implies that replicates used in inferential statistics are dependent (Hurlbert, 1984). Here, the position of an animal at time $t + \Delta t$

Table 5.1. Number of locations (class 2 and 3; with 0–350m accuracy) for the collared elephants in each season in Tembe Elephant Park and southern Mozambique. The values in brackets are the respective Schoener ratios measuring the serial autocorrelation of the location data.

	Wet season 1	Dry season 1	Wet season 2	Dry season 2
Tembe Elephant Park				
Bull	320 (0.31)	132 (0.20)		
Breeding herds	270 (0.26)	195 (0.29)	181 (0.34)	316 (0.42)
Breeding herds	288 (0.31)	212 (0.34)	196 (0.37)	355 (0.34)
Breeding herds	153 (0.63)	100 (0.32)	86 (0.82)	165 (0.46)
Southern Mozambique				
Bull	203 (0.08)	186 (0.03)	162 (0.09)	48 (0.38)
Bull	209 (0.13)	164 (0.04)	156 (0.41)	259 (0.18)
Bull	118 (0.46)	96 (0.13)	109 (0.30)	264 (0.05)
Breeding herds	145 (0.27)	105 (0.45)	71 (0.14)	231 (0.26)
Breeding herds	247 (0.19)	192 (0.26)	185 (0.27)	308 (0.21)

is dependent of its position at time *t*, so that we can predict an animals position based on its previous position. We assessed the level of autocorrelation of the location data with the Schoener's ratio, following Swihart & Slade (1985). When the ratio is < 2, the location data are serially autocorrelated (Swihart & Slade, 1985).

We used the compositional method (Aebischer, Robertson & Kenward, 1993) to analyse seasonal second and third order (see Johnson 1980 for a detailed description of terminology) landscape selection. Second order selection relates the proportional use of landscape patches within each elephant's home range relative to its availability in the total elephant range. Third order selection reflects on the relative number of location points in each landscape patch within each elephant home range. We define availability as the proportional contribution of each landscape in the total elephant range. We replaced missing values (landscapes with zero values) with 0.001, which is one order of magnitude lower than the lowest proportional value in the usage of landscapes (following Aebischer *et al*., 1993).

The studies we collated used one of three approaches to estimate home range sizes. These included individual recognition (mark-recapture methods), VHF radio and satellite/ GPS based platforms (e.g. Leuthold, 1977; Dunham, 1985; Douglas-Hamilton, 1998). These methods reported 3 to 1051 locations per individual elephant over periods ranging from 3 to 24 months. We omitted estimates that used less than 30 location points (based on Seaman *et al*., 1999). We $\log_{10}$–transformed all home ranges and rainfall data before analysis (Sokal & Rohlf, 1995) and distinguished between fenced and unfenced elephant populations.

Results

Our satellite-tracking database yielded a mean (±SD) of 189 ± 77.3 elephant locations per season for each individual in southern Mozambique and TEP. Mean seasonal home range area stabilised at 136 ± 65.9 locations and we consider our estimates robust. All the elephants in this study location data were serially autocorrelated, that is, the Schoener ratios for all the individuals range from 0.03 to 0.82 (Table 5.1).

Elephant bull(s) had larger home ranges than breeding herds in both TEP and southern Mozambique (Table 5.2). The dry season home ranges for both sites were also smaller than in the wet seasons but, with the exception of the elephant bull in TEP not as prominent, as documented elsewhere. Irrespective of season and sex of the elephant, home ranges in TEP, were at least three times smaller than for those elephants in southern Mozambique.

Table 5.3 compares the second and third order selection of the elephants in our study. During our study, elephants in southern Mozambique used closed woodlands more than expected relative to its availability. These elephants did not show any preference for reed beds, open woodlands and sand forests. However, if we compare the relative number of locations of elephants in their respective home ranges, sand forests ranked first, non-significantly in the wet and significantly in the dry seasons. Again, the number of locations in the rest of the landscapes was relative to their availability within the elephants' home ranges.

The overall pattern in elephants' landscape use in TEP is less clear. Only in the wet seasons, did closed and open woodlands rank higher in their relative use than sand forests and reed beds. There is, however, no detectable difference between the two woodland types, or between sand forests and reed beds. In the dry season, elephants did not use any landscape more than expected by its availability. However,

Table 5.2. Mean (±SD) seasonal home ranges (km^2) calculated with 95% Minimum Convex Polygon for breeding herds and bulls in Tembe Elephant Park and southern Mozambique for the wet and dry seasons. (*n* represents the number of individuals).

		Tembe Elephant Park	Southern Mozambique
Herds	Wet seasons	139.3 ± 79.2 (*n* = 3)	353.9 ± 104.2 (*n* = 2)
	Dry seasons	80.0 ± 9.5 (*n* = 3)	253.7 ± 109.3 (*n* = 2)
Bull(s)	Wet seasons	295.7 (*n* = 1)	716.9 ± 327.6 (*n* = 3)
	Dry seasons	139.6 (*n* = 1)	639.3 ± 223.5 (*n* = 3)

Table 5.3. Hierarchical second (a) and third (b) order landscape selection for elephants in (i) Tembe Elephant Park and (ii) southern Mozambique. (SF = Sand forest, CW = Closed woodland, OW = Open woodland and RB = Reed beds).

	(i) Tembe Elephant Park	(ii) Southern Mozambique
(a) Second order landscape selection		
Wet seasons	CW = OW >>> SF > RB	CW >>> RB > OW > SF
Dry seasons	SF > RB > CW > OW	CW >>> RB > OW > SF
(b) Third order landscape selection		
Wet seasons	SF > OW > CW > RB	SF > RB > CW > OW
Dry seasons	OW > CW > SF >>> RB	SF >>> RB > CW > OW

= Equal preference, > NS preference ($P>0.05$), >>> Significant preference ($P<0.05$)

when we compare number of location points relative to landscape availability within their respective home ranges, elephants used the reed beds significantly less in the dry season. Finally, in the wet season, elephants used the landscapes relative to their contribution within the individual home ranges.

We collated sufficient information on elephant home ranges from ten studies that yielded data on home range areas for 93 individuals across southern Africa. The CERU database provided information on a further 52 and this study nine elephants. Mean annual rainfall between the sites ranged from less than 100 up to 1200 mm.a^{-1}. Elephant home range decreased significantly with an increase in mean annual rainfall ($F_{1,151}$ = 112.08; $P < 0.0001$; $r^2 = 0.43$) (Fig. 5.2), with no significant difference between fenced and unfenced study areas ($F_{1,151}$ = 0.44; $P = 0.51$).

Discussion

The elephant population in Maputaland functioned as a singular entity before its fragmentation by the fences erected around Tembe Elephant Park between 1983 and 1989. The electrified elephant-proof fence that spans the Mozambique-South Africa border effectively divided the population into two fragments. The elephants in southern Mozambique remained unfenced and could therefore roam freely. The scenario here is very similar to that elsewhere across sub-Saharan Africa, where electric fences restrict the movements of elephants (Addo Elephant National Park, Kruger National Park). High densities of people may also hinder free passage (e.g. Hoare & du Toit, 1999; O'Connell-Rodwell *et al.*, 2000). Restriction conceivably may reduce home range sizes, thereby increasing the intensity of landscape utilisation and the apparent impact of elephants. Home ranges, however, are known to be influenced by elephants' social interactions, landscape heterogeneity and rainfall (e.g.

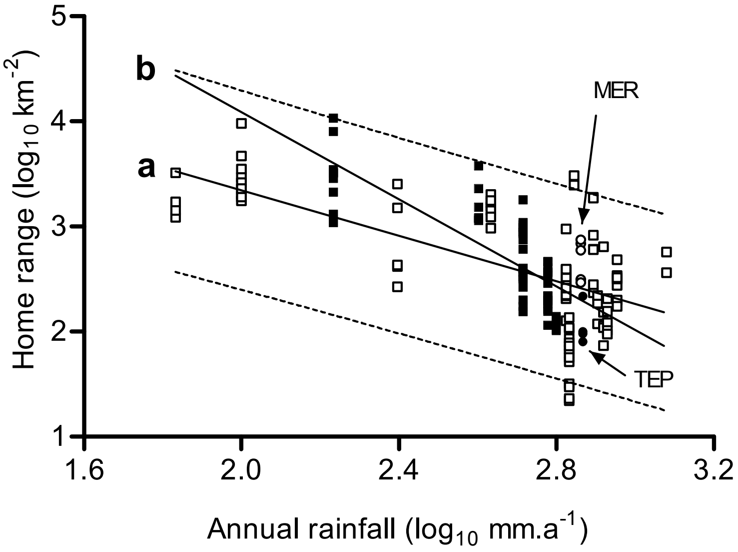

Figure 5.2. Elephant home ranges decrease significantly with an increase in mean annual rainfall for both the unfenced (open squares/ line marked **a**) and fenced (filled squares/ line marked **b**) elephant populations. Arrows indicate the home range sizes of elephants in southern Mozambique (closed circles) and Tembe Elephant Park (open circles). Regression lines are only for illustrative purposes and the dashed lines indicate the 95% confidence interval for the unfenced elephant populations.

Verlinden & Gavor, 1998; Charif *et al*., 2005; Grainger *et al*., in press). Our study across Maputaland, where the rainfall is similar, excludes such influences. With a component of the elephant population restricted by fences, while the other roamed freely, we had an opportunity to assess the influence of restriction on range use. By addressing the apparent impact of confinement in view of the relevance of rainfall variation elsewhere across southern Africa, we could further assess the consequences of restriction on home range use.

The importance of location data being autocorrelated attracts a large amount of attention in the ecological literature (*e.g.* Schoener, 1981; Swihart & Slade, 1985; Legendre, 1993; Hansteen, Andreassen & Ims, 1997; Rooney, Wolfe & Hayden, 1998; de Solla, Bonduriansky & Brooks, 1999). This debate divides between statistical (Schoener, 1981; Swihart & Slade, 1985) and biological relevance (Rooney *et al*., 1998; de Solla *et al*., 1999) of spatial and temporal autocorrelation. Statisticians suggest sub-sampling the data by increasing the time-period between location points until achieving independence – known as time to independence (TTI) (Swihart & Slade, 1985). However, de Solla *et al*., (1999) argue that such a destructive sub-sampling scheme reduces significant biological relevance. They base their argument on the infrequent sampling procedures, such as ‘bursts’ of location points with variable time-periods between sampling occasions. We obtained our elephant location data systematically at regular time intervals (Rooney *et al*., 1998; de Solla *et al*., 1999). Besides Cushman, Chase & Griffin (2005), no previous study on elephant space or landscape use incorporated the influence of autocorrelation in interpreting their results. Increasing the time-periods between location points in their study did not decrease autocorrelation (Cushman *et al*., 2005). They did show, however, that the complex pattern of elephants’ space use behaviour is linked to the onset of regional rainfall. This example highlights the biological relevance of autocorrelated data (see de Solla *et al*., 1999).

Elephants confined to the TEP have smaller home ranges than those roaming freely across southern Mozambique. This was irrespective of sex and season, or despite the similar rainfall patterns between sites during our study. For example, breeding herds in southern Mozambique had home ranges comparable to the total size of TEP, whereas those in the Park only used a third of the area available to them. This is the same as elephants living elsewhere under similar conditions, such as in Addo Elephant National Park (103 km^2) and Pilanesberg National Parks (500 km^2), where elephants use between 10-50% of the available area (Whitehouse & Schoeman, 2003; Slotow & van Dyk, 2004). However, home ranges of elephants in southern Mozambique for this study are also three times larger than a previous assessment for elephants in this population (Ntumi *et al*., in press). Both studies used satellite technology and the 95% MCP in calculating home ranges, using a similar delineation of seasons and rainfall. Sample sizes (number of individuals collared) for both studies are low, and differences may reflect normal variation in elephants' home range in southern Mozambique. From this we may conclude that the home ranges of elephants not constricted by fences in Maputaland vary more than confined elephants.

Landscape selection by elephants in Maputaland confirms their general widespread and catholic requirements. Elephants in southern Mozambique use reed beds and closed woodlands more than expected by their availability alone, with the rest of the landscapes used non-selectively throughout the year. Our results differ from de Boer *et al*. (2000) and Ntumi *et al*. (in press), both whom indicated sand forests and the Futi flood plains to be the preferred landscapes for elephants in southern Mozambique. However, de Boer *et al*. (2000) and Ntumi *et al*. (in press) only differentiate between forests and open woodland, with closed woodlands incorporated into the sand forests. Their observation that elephants prefer sand forests therefore may principally be due to them attending to closed woodlands or forests other than sand forests.

In spite of the similarities between the study conditions, i.e. the spatial extent (area of coverage), studies differed in formulating the landscape information (Lillesand & Kiefer, 2000). In their preference assessment, both de Boer *et al*. (2000) and Ntumi *et al*. (in press) relied on maps where polygons, rather than raster data, defined the landscape units onto which they placed the elephants' locations. These homogenous units have a lower spatial resolution and contain inherently less information (Lillesand & Kiefer, 2000). Here, the 'user defined decision rules' (Lillesand & Kiefer, 2000) applied after landscape classification may cause small patches of a particular landscape, often important to an elephant to be masked by the dominant single landscape type of the area (Lillesand & Kiefer, 2000). Maputaland is very heterogeneous at the finest landscape resolution and using raster data (at the 25 X 25 m pixel resolution), we managed to retain this regional heterogeneity. We therefore consider our landscape preference analysis of elephants for this region to be more robust.

The confinement of elephants to TEP changes the proportional availability of landscapes in Maputaland to them, and the provision of water may further disrupt their selection patterns. Surface water in southern Mozambique is not a limiting factor, and management does not provide artificial water. Elephants in southern Mozambique were consistent in their landscape selection patterns throughout the study period. This is in contrast to TEP, where the landscape selection of elephants is less clear. In fact, our results only indicate elephants to avoid reed beds during the dry season. Reed beds in the Muzi swamps in TEP are associated with natural surface water. Elephants are water dependent (Sukumar, 2003), and their avoidance of these areas during the dry season is against expectations. This may be a response on the provision of artificial water that characterised TEP during our study period.

Home range areas of elephants decreased with an increase in mean annual rainfall. Our results agree with Osborn (2004) and Sukumar (2003)), who related the home ranges of males and females separately with rainfall. Rainfall may not be the sole variable that elephants respond to, since rainfall is positively related with primary productivity and herbivore biomass in savanna systems (e.g. Phillipson, 1975; Coe, Cumming & Phillipson, 1976; Bell, 1982; East, 1984; Fritz & Duncan, 1994; Fritz *et al.*, 2002). Consequently, primary productivity rather than rainfall may be a determinant of elephant home range size.

From our results, constricting elephants, such as in TEP, did not significantly influence the home range sizes along the rainfall gradient. However, our analysis has limitations, often associated with these quantitative assessments (Gates, 2002). More studies reported on range use of elephants in the mesic than arid and sub-tropical regions. The rainfall range against which we predicted enclosed elephants' space use was narrower than the free roaming populations. Another factor is that of estimating elephant home ranges using different sampling and statistical methods (e.g. White & Garrott, 1990). We excluded home range estimates of some 40 elephants due to insufficient sampling or statistical reporting. Often studies did not report on the study duration, sample size (both number of individuals and locations per individual), frequency of data acquisition, or partitioned between the sexes and seasons. These variables may influence the overall interpretation of elephants' space use patterns (e.g. Hall-Martin, 1987; Thouless, 1998).

The limitations mentioned above lead us to visually assess the rainfall-home range relationships. Home ranges areas for elephants confined by fences in arid regions appear to be larger than the free roaming populations. The opposite is true in the mesic regions, which induce a steeper decline in the slope in this relationship. Again, the systematic placement of waterholes in confined areas may explain this, since we know that these influence range use (see Grainger *et al*., in press). Artificial waterholes in the drier regions may provide opportunity for elephants to expand their home ranges as resources deteriorate. It may also allow elephants in mesic regions to remain in areas beyond which may be permitted by primary production. Both cases allow elephants to use areas for extended periods, and not give vegetation the opportunity to recover from impact induced by elephants.

We conclude that fences and the artificial provision of water may disrupt space utilization and landscape preference of elephants in TEP. However, home ranges sizes are within the expected variation allowed for by rainfall. Elephants in southern Mozambique have however, higher variation in space utilization that may negate the potential negative impact they have on vegetation.

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Chapter 6

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A meta-analysis of elephant impact

Robert A.R. Guldemond and Rudi J. van Aarde

Over most of Africa, elephant numbers have declined in the previous two centuries. Yet, those managing the 260,000 elephants in southern Africa often consider culling them as high elephant numbers are deemed harmful to biological diversity. Our review of scientific studies does not support this notion. A handful of studies dominate the literature. These show that elephants have a negative effect on tree densities. Short-term studies show that elephants have an immediate effect on plants. Long-term studies do not support this notion. Elephants also do not decrease the diversity of other species present in the system. The underlying premise for culling elephant is not justified.

Keywords: elephant impact; perceptions; plants; diversity; scale

1. INTRODUCTION

Across Africa, hunting and poaching have drastically reduced the number of elephants (*Loxodonta africana* Blumenbach and *L. cyclotis* Matchie) (Spinage 1973; Stiles 2004). The establishment of protected areas, their fencing and the provision of water has allowed elephant populations to rebound (Douglas-Hamilton 1987; Caughley *et al*. 1990). Fencing conceivably interfered with the role dispersal has in controlling population growth (see Chafota & Owen-Smith 1996) and water provision may enhance survival of juvenile elephants (Shrader *et al.* in review). Confining high densities of elephants may transform woodlands into shrublands or grasslands that may induce local disappearances of other species. This is what Caughley (1976) and others referred to as the "elephant problem". Examples include Dublin *et al.* (1990), Cumming *et al*. (1997), Trollope *et al*. (1998), van de Vijver *et al*. (1999) and Western & Maitumo (2004).

At issue is whether managers should reduce elephant numbers to maintain biological diversity (e.g. Whyte *et al.* 2003). Several sub-Saharan conservation authorities have opted to cull elephants (Feely 1965; Pienaar 1966; Astle 1971; Hanks *et al*. 1981; Whyte *et al*. 1999). Gillson & Lindsay (2003), Goheen *et al*. (2004), Skarpe *et al*. (2004) and Wiseman *et al*. (2004) provide an alternative opinion. The impacts of elephants on vegetation depend on a large number of confounding variables. Global climate change, frequent fires, drought, disease and trampling may also reduce tree densities and transform woodlands into grasslands (e.g. Walker *et al*. 1981; Noy-Meir 1982; Gillson 2004).

We used meta-analytic techniques (Cooper & Hedges 1994) to synthesize the impact of elephants on components of biological diversity. We

(1) Establish which studies were most influential in shaping opinion on the impact of elephants,

(2) Investigate what effects elephants have on vegetation,

(3) Establish if elephant also affects other components of savannas, such as vertebrates and insects,

(4) Investigate how the duration of the study and selection of response variables influenced the published findings.

Our results suggest that a biased citation of selected studies generated current perceptions. Certainly, elephants have adverse effects on individual plants. Despite that, we found that most evidence is inconclusive for the general negative impact on vegetation, other vertebrate and insect taxa.

2. METHODS

Computerised databases, references lists and the African Elephant Bibliography (http://www.elephant.chebucto.net/index.cgi) provided the information for our analyses. We considered only primary studies published up to 2004 in English peer-reviewed journals. To reduce dependence and bias we excluded symposium presentations and abstracts, newsletters, books and chapters in books, post-graduate theses and internal reports. We excluded studies conducted under artificial conditions such as zoological gardens and the response of exotic species to elephants. We documented the year of publication, study site, duration of the study, the design (e.g. replication and controls), and the number of times each study was subsequently cited. Author opinions were grouped into negative or non-negative (positive, neutral) classes.

Finally, we grouped together the response variables used by the studies into (1) individual plant structure (e.g. cover, height, crown/ basal diameter), (2) damage indices (percentage debarking, canopy removals) (3) population (densities, mortality, survival) and (4) community variables (diversity indices) separately for plants, vertebrates (mammals and birds) and insect taxa. For convenience in discussing our results, we will call all reductions in abundance, density, biomass cover, species richness etc, plus all increases in damage, as "reductions in abundances". That is, henceforth, "abundance" becomes a catchphrase for all the various ways in which elephants affect other species.

3. ANALYSIS

We developed a standardised ranking score for each study to ascertain the most influential studies. The mean difference between the age of a given study and those that cited it, were divided by the age (in years) of that study. We then divide this value by the number of times that it was cited. Consequently, the highest ranked studies were those cited most frequently and for the longest available period since its publication.

We used Cohen's *d* (Gurevitch & Hedges 1993) to calculate the effect sizes separately for experimental (with elephant exclusion control plots) and observational studies (those without). We interpret the overall effect size as the "reductions in abundances" elephants have for the taxa. For experimental studies, Cohen's *d* is the difference in the response variable between treatment (elephant presence) and control (elephant absence), divided by the pooled average standard deviation (Gurevitch & Hedges 1993). For those studies that assigned elephant presence as controls in their study designs, we reassigned the published information as treatment values. In the studies without controls, we divided the pooled average standard deviation by the difference in values of response variables between the beginning and end of each study. Only studies that reported sample sizes and indices of variability around the mean could be included in these analyses. Large differences and low variability will result in larger effect sizes (Gurevitch & Hedges 1993).

We used the *Q*-statistic in a mixed model analysis of variance to investigate heterogeneity amongst response variables. The *Q*-statistic is a measure of the degree to which the study outcomes (in this case Cohen's *d*) of the response variables share a common effect size (see Gurevitch & Hedges 1993 for further details). Here we defined the analysis units (*k*) as all the extractable response variables published in each study. Using the rank-correlation method of Begg & Mazumdar (1994) and calculating the 'fail-safe number' of Rosenthal (1991), we assess publication bias for the effect size values. The number of published response variables with non-significant outcomes in order to nullify the overall effect size constitutes the 'fail-safe number'. This serves as a measure of the robustness of the meta-analysis.

4. RESULTS

Our search yielded 230 articles in 57 journals published from 1961 to 2004 (Appendix B). The number of papers published per year increased with time ($F_{1,43} = 98.63$, $p < 0.0001$) and covered 72 sites across sub-Saharan Africa. Most studies (80.1%) lasted fewer than five years. Only 15.1% of the published studies included controls, that is, areas without elephants.

The 20 most influential publications account for 50.9% of all citations in our database (table 6.1), the rest of the 230 articles share the remainder. These highly ranked publications had a mean age of 27 ± 9.8 (SD) years, but age had no significant

Table 6.1. The twenty most influential publications, the number of times studies in our database cited them and the calculated importance ratio for each study.

Study	Number of citings	Importance ratios
1. Laws 1970	60	37.1
2. Caughley 1976	57	34.9
3. Buechner & Dawkins 1961	44	25.7
4. Anderson & Walker 1974	33	24.7
5. Van Wyk & Fairall 1969	31	21.9
6. Dublin *et al*. 1990	34	21.1
7. Pellew 1983	30	18.0
8. Croze 1974	29	17.7
9. Barnes 1983	28	17.1
10. Wing & Buss 1970	30	16.4
11. Jachmann & Bell 1985	24	15.7
12. Jachmann & Croes 1991	15	10.0
13. Cumming *et al*. 1997	16	9.4
14. Ben-Shahar 1993	17	9.0
15. Glover 1963	18	8.7
16. Field 1971	19	8.4
17. Thompson 1975	13	8.2
18. Leuthold 1977	14	7.3
19. Penzhorn *et al*. 1974	11	7.0
20. Guy 1981	11	6.8

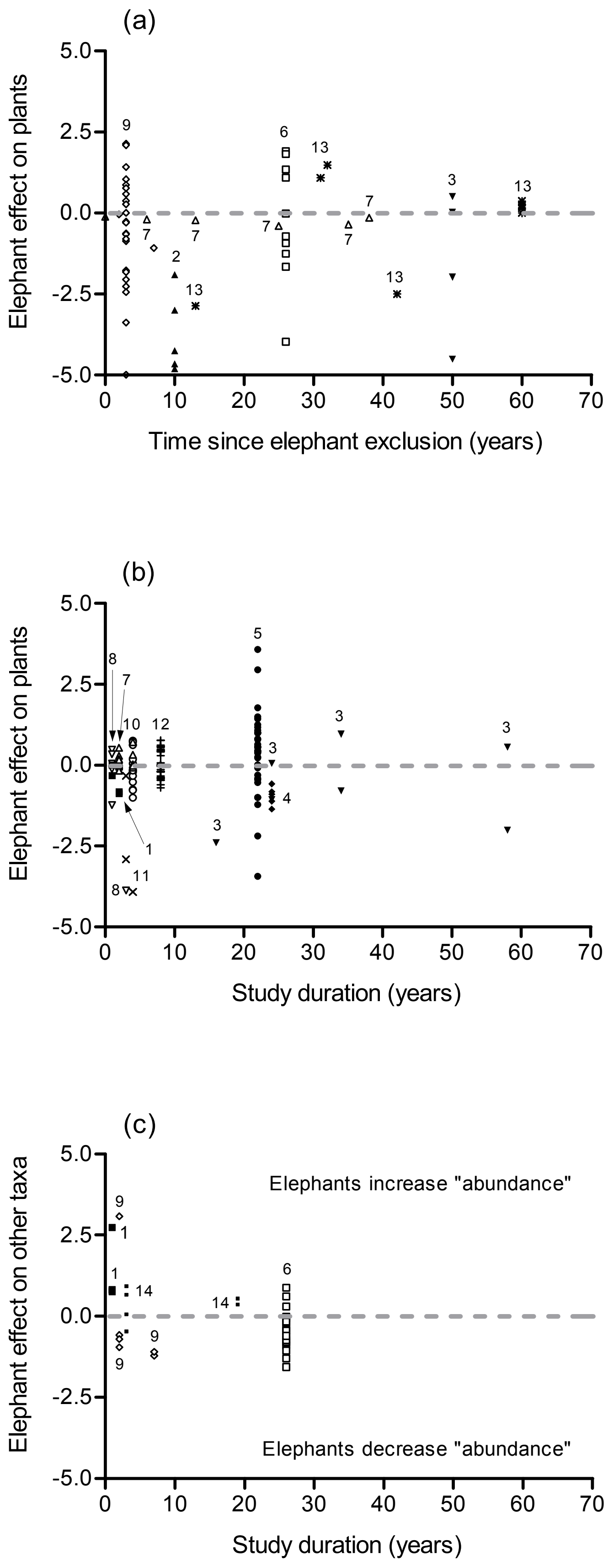

Fig. 6.1 Elephants either increase and/ or decrease plant “abundance” in

Fig. 6.1 (continue) experimental (a) and observational (b) studies. Other vertebrate and insect taxa (c) show a similar pattern for all the studies combined. Data points above the horizontal dashed line in each figure represent where elephants increase "abundance" – see methods for details. Numbers on the graphs represents the different study sites; 1 = Northern Botswana, 2 = Sweetwaters Game Reserve, 3 = Kruger National Park, 4 = Murchison Falls National Park, 5 = Kibale National Park, 6 = Mana Pools National Park, 7 = Sengwa Wildlife Research Area, 8 = Nazinga Game Reserve, 9 = Mpala Research Centre, 10 = Tsavo National Park, 11 = Amboseli National Park, 12 = Ithala Game Reserve, 13 = Addo Elephant National Park, 14 = Tembe Elephant Park. Data from Augustine & McNaughton 2004; Barnes 2001; Birkett 2002; Botha *et al*. 2002; Buechner & Dawkins 1961; Chapman *et al*. 1997; Cumming *et al*. 1997; Eckhardt *et al*. 2000; Fenton *et al*. 1998; Goheen *et al*. 2004; Guy 1981; Herremans 1995; Jachmann & Croes 1991; Keesing 1998; Leuthold 1977; Lombard *et al*. 2001; Mapaure & Campbell 2002; McGeoch *et al*. 2002; Musgrave & Compton 1997; Novellie 1988; Parker & Witkowski 1999; Western & Maitumo 2004; Wiseman *et al*. 2004.

influence on its ranking ($F_{1,18} = 3.22$, $p = 0.089$). Sixteen of these influential studies concluded that elephants had decreased abundance of taxa. (We use abundance in the special sense defined above). A significantly lower number (56%) of all 230 studies came to the same conclusion ($\chi^2 = 5.50$, 1 d.f., $p < 0.01$).

Only 15 experimental ($k = 86$) and 13 observational ($k = 141$) studies published adequate information for our meta-analyses. For all the taxa combined, our results show that elephants do not affect their abundances ($d = -0.07 \pm 0.01$, $p < 0.05$, 95% CI: -0.20 to 0.46, $k = 227$). However, when consider separately, experimental studies indicate that elephants significantly decrease plant abundance ($d = -0.50 \pm 0.03$, $p < 0.05$, 95% CI: -0.19 to -0.81, $k = 59$). With the observational studies (no elephant exclusion), elephants increase plant abundance non-significantly ($d = 0.04 \pm 0.01$, $p < 0.05$, 95% CI: -0.11 to 0.19, $k = 132$). Elephants further, had no apparent effect on taxa other than plants (e.g. mammals, birds and insects; $d = -0.08 \pm 0.03$, $p < 0.01$, 95% CI: -0.40 to 0.23, $k = 34$).

Study site characteristics may also influence these outcomes. While most of the data for plants show that elephants decrease abundance, for sites 6, 7, 9 and 13, there is no consistent pattern (figure 6.1a). At these sites, there are equal increases and decreases in plant abundance. Interestingly though, duration of experimental studies also influence outcomes – those conducted over a short duration showed decreases in abundance. Longer studies showed either no overall effect or even increase in abundance. The study at site 3 (figure 6.1a), where elephants reduce plant abundance over a 50-year period, suffered from poor replication (n = 2).

Similarly, for the studies without controls (figure 6.1b), plant variables tended towards an equal distribution of increasing and decreasing plant abundance (sites 5, 7, 8, 10 and 12), irrespective of time-period. In addition to this, the initial overall increase in abundance elephants have for other taxa, such as for insects, also seems to decline with study duration, with study site 6 having equal responses above and below the neutral effect line (figure 6.1c). In general, though, study site confounds the result — studies with short duration are at different sites than studies conducted over longer periods.

It is clear from figure 6.1a-c that plants and other taxa vary greatly in their responses to elephants (amongst plants: $Q = 1956.6$, 225 d.f., $p < 0.0001$; between taxa: $Q = 492.3$, 2 d.f., $p < 0.0001$). Studies that focussed on how elephants decrease plants abundance mostly (90%) concentrated their efforts at individual (structural) and population (mortality and survival) indices. This is in contrast to those investigating the decrease in abundance for other taxa, with 70% of the responses reported at the community level.

Publication bias is prevalent in experimental studies ($r_s = -0.31$, $p < 0.001$), but not for observational studies ($r_s = 0.04$, $p = 0.54$). However, the 'fail-safe' number for experimental (2696) and observational studies (6883) both exceeded the number of published variables necessary to nullify the overall effect size (570 and 1065 respectively). We therefore consider our assessment robust.

5. DISCUSSION

The elephant-diversity debate is contentious. Elephants' inducing structural changes in woody plants largely fuels the debate (e.g. Dublin *et al.* 1990; Cumming *et al.* 1997; Ben-Shahar 1998). Although savannas are in a continuing state of flux (Gillson 2004; Stephenson 2004), some consider such changes as unacceptable (Pienaar *et al.* 1966; Astle 1971; Cumming *et al.* 1997; Whyte 2004). However, support for the standpoint is not universal (e.g. Gilson & Lindsay 2003). Our meta-analyses challenge some of the existing perceptions of the consequences elephants may have for savannas.

Interest and studies on the "elephant problem" have increased since 1961. A fraction of publications (20 of 230) dominates the debate on impact, as more than half the pertinent literature refers to them. This bias towards citing papers concluding that elephants have a negative effect on vegetation, may partly explain some of our current perceptions and interpretations of the "elephant problem". Citation bias is common in science (Gates 2002). Factors include the directionality and magnitude of results, journal quality, article length, number of authors per article and institutional prestige (Møller & Jennions 2001; Murtaugh 2002; Leimu & Koricheva 2005). We argue that the interpretation in the directionality of results has contributed to the bias in the elephant-diversity debate.

This is of concern as it provides a rationale for conservation bodies to justify reducing elephant numbers as a management activity (e.g. Feely 1965; Pienaar *et al.* 1966; Astle 1971; Hanks *et al.* 1981; van Aarde *et al.* 1999; Whyte 2004) with political and economic implications (e.g. Bulte *et al.* 2004; Hambler *et al.* 2005). Our assessment shows that only half of all studies concluded that elephants had negative consequences for components in their environment. Management driven by an unbiased assessment should also consider the positive effects of elephants (e.g. Cochrane 2003; Goheen *et al.* 2004).

Our assessment supports the notion that elephants have a significant effect on plants. This makes sense as through feeding, they damage individual trees, shrubs and seedlings (e.g. Barnes 1980, 1983; Lewis 1986; Jachmann & Croes 1991). The impacts of elephants on plants are largely immediate, and this may contribute to short-term studies illustrating a negative effect. Such short-term studies that continued for less than five years dominate (80%) our database and may ignore the recovery of vegetation. This is not unique, as short time periods dominate ecological studies in general (see Weatherhead 1986; Tillman 1989). Our analyses agree with Caughley (1976), Dublin (1991), Lock (1993) and Leutholds' (1996) assertions that increased study duration eliminates the apparent negative impact of elephants. Based on short-term studies, the ecological conclusions we reach, as well as our subsequent management actions, are biased and may be inappropriate.

The effect of elephants differs between the taxa included in our analyses (see Q-statistics). It is therefore inappropriate to consider the impact on one taxon as representative across other taxa, or on biological diversity. In addition, one cannot separate the responses measured in elephant studies from the contribution made by other herbivores or events such as fire and rainfall (e.g. Ben-Shahar 1998; Dublin *et al.* 1990; Cumming *et al.* 1997; Trollope *et al.* 1998; van de Vijver *et al.* 1999). Responses may also vary from site to site, further confining the interpretation of findings and the role of elephant in African savannas. One should consider the 'full suite' of community level responses. This may alter the perspectives of studies focussing on single species or even taxa. Only seven of the studies included in our assessment, however, reported response to elephants at this level. We need more information before we can comment on the consequences elephants may have at the community level. We found no overall support for the notion that elephants reduce species diversity (Cumming *et al.* 1997; Whyte 2004), despite their apparent adverse effects for individual plants. It is naive to link their apparent impact on individual plants to biological diversity in general. We therefore conclude that the interpretation of selected studies generate current perceptions.

Future quantitative assessments must rely on rigorous experimental protocols (for example Underwood 1997; Quinn & Keogh 2002) that include a range of spatiotemporal scales (Levin 1992; May 1994), the investigation of all relevant response variables (this study) and appropriate statistical information (Gurevitch & Hedges 1993). We disregarded half of all the studies in this meta-analysis that had proper experimental designs, but lacked sufficient statistical reporting.

Equilibrium based agro-economic arguments dictate the debate surrounding elephant management (confine movements, alleviate environmental constraints and impose constant values on animal populations; e.g. Macnab 1985). This no longer makes sense and we need to allow scale-dependent processes (Lewin 1986; Western *et al*. 1989) to drive conservation management (Gillson & Lindsay 2003). These may include plans to allow acting out dispersal and meta-population dynamics by establishing sink populations through range expansion into marginal areas. This could also allow for seasonal alleviation of 'high' elephant densities on a temporal scale, and initiates recovery periods for other components part of the larger system.

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Chapter 7

Synthesis

Conservation management changed greatly over the last four decades (e.g. Western 2003). One such change involves the management of elephants. Priorities shifted from treating elephants as an endangered species (Douglas-Hamilton 1987; Caughley *et al*. 1990) to situations where some regard them as a commercially exploitable species (Leader-Williams *et al*. 2001; Stiles 2004; Bulte *et al*. 2004; Hambler *et al*. 2005). The situation arises when measures such as fencing conservation areas and the provision of artificial water allow elephant numbers to increase (for a review on recent trends in elephant numbers see Blanc *et al*. 2005). Current concerns revolve around local elephant densities exceeding the so-called 'ecological carrying capacities' of protective areas (e.g. Gillson & Lindsay 2003). This prompted one of the central questions amongst conservationists today – what are the consequences of confined elephants for these fenced conservation areas?

The issue at hand is whether conservation management should intervene and prevent elephants from destroying components of biodiversity, and if so, how (e.g. Cumming *et al*. 1997; Whyte 2004). This issue is by no means new, shortly after the cessation of World War II, Eggeling (1947) pointed to the destruction that elephants caused in the rainforests of Uganda. The matter remains unresolved, with wildlife managers continually seeking justification for the control of elephant numbers (e.g. Whyte 2004). Appendix B provides the most comprehensive reference list of peer-reviewed studies dealing with this topic up to December 2004.

The Tembe Elephant Park in Maputaland is another place with a potential 'elephant problem'. The Park is fenced, and apart from elephants, supports a unique sand forest ecotype (Kirkwood & Midgley 1999; Matthews *et al*. 2001). This forest type is high in species diversity and contains many endemic species (van Rensburg *et al*. 1999, 2000; Haddad 2003). Elephants may threaten this diversity and endemicity as well as those of the mixed woodlands in the Park (see Matthews *et al*. 2001; McGeoch *et al*. 2002). My study aimed at addressing these concerns and to give some insight into the concept of 'elephant impact'.

I relied on the comparative approach while studying the influence of elephants at different scales. This approach strengthened my assessment of the impact elephants may have had for some plant variables at different scales. I distinguished between the micro-, meso-, and macro scales and used a meta-analysis to determine differences in local, regional and the overall effect of elephants. For the micro- and meso scales, I studied the effect elephants had for plants and plant communities in the Tembe Elephant Park. The macro scale assessment reflected on how confined elephants responded to space and landscapes, and how such information can be used to formulate alternative management options for elephants. The meta-analysis included response variables for plants, insects, birds and mammals across Africa.

At the micro scale level (Chapter 3), I focussed on the potential consequences tree canopies altered by elephants have for sub-canopy vegetation. The response of such plants depended on vegetation type – in closed woodlands, elephants created gaps in the canopy and this allowed grass species to establish. In these gaps the woody saplings could also reach the upper canopy strata. In the open woodlands, elephants created conditions similar to the areas where no trees were present. Here, species not normally associated with canopies, may be replaced by shade-tolerant species. Therefore, at the local level, elephants increased heterogeneity in the closed woodlands, but homogenised open woodlands.

At the meso scale (Chapter 4), I compared woody plant community variables for sand forests, and the open and closed woodlands inside the Tembe Elephant Park to similar plant communities outside the Park. Species composition for all three of the landscape types differed significantly between the areas inside and outside of the Park. However, tree and shrub densities, abundance-incidence and rank-abundance relationships did not differ when comparing sample sites inside and outside the Park. Elephants may have had little impact at the regional and landscape level. On the other hand, larger scale events such as droughts, fire and seed dispersal may have masked the impact elephants had for these plant community variables.

At the macro scale (Chapter 5), I studied the effect that the fencing of Tembe Elephant Park had on the home ranges and landscape selection of elephants. I used a rainfall gradient to interpret my findings on the variability of home range sizes across southern Africa. The analysis of landscape preference focused on comparing confined elephants living in the fenced off Tembe Elephant Park with the free ranging elephants living in southern Mozambique (those occurring in Maputo Elephant Reserve and along the Futi River). Elephant home ranges in the Park were a third of the size of those of elephants occurring in southern Mozambique, but still falls within the range of sizes predicted by the rainfall gradient implied by studies conducted across southern Africa. Landscape selection patterns, however, differed between the two elephant groups – in southern Mozambique, elephants preferred closed woodlands throughout the study period. In the Tembe Elephant Park, elephants show no clear preference, except for avoiding the Muzi Swamp in the dry season. This is against expectation, as elephants are a water-dependent species, and the swamps contain reed beds and natural surface water. The provisioning of drinking water under these confined conditions may influence the way that elephants use the area – this may have consequences for biodiversity.

The meta-analysis (Chapter 6) focussed on the impact that elephants have on their environment. Here I investigated how the interpretation of published results on elephant impact shaped perceptions. Twenty of the 230 peer-reviewed articles I collated (listed in Appendix B) dominated the literature with more than 50% of the total citations referring to these. The remaining 210 articles shared the remainder, with 70 of these receiving no citations. Sixteen of the dominant 20 studies concluded that elephants had a negative effect on plants. My results showed that studies conducted over shorter periods concluded that elephants affect other species negatively – long-term studies did not support this. However, I acknowledge that site-specific characteristics influence the overall outcomes, as sites with short-term studies were different from those with long-term studies. This holds for both experimental and observational studies. A further caveat is that researchers have chosen different response variables and focal taxa. For instance, studies based on vegetation responses used response variables that showed immediate effects after an elephant fed on a tree, such as damage indices, measurement of structural changes, decrease in abundance and mortality rates. Studies on birds, insects and small mammals tended to focus on community parameters. Intuitively this too makes sense – elephants do not feed on them, so damage indices and mortality rates are unrealistic. Community indices in general are due to their character, more likely to show less of an elephant effect.

To summarise, elephants had a combination of positive, neutral and negative effects on plant variables at the micro- and meso scales in Tembe Elephant Park. It is clear that responses to elephants vary, which motivated the meta-analysis. With this, I was able to show that one should consider a large number of aspects in the design and interpretation of elephant impact studies. These include the methods employed, the response variables used, whether the study design controlled confounding factors and the study duration. Study site characteristics, such as mean annual rainfall, the dominant soil types and aspects of fire and water management may play an additional role. Interpretation should consider other stochastic and deterministic processes, such as those associated with climate change; this leads me to ask what do these meta-results mean for the managers of the elephants in the Tembe Elephant Park?

The results of my thesis were not included in the meta-analysis, as it is only currently been evaluated for publication in peer-reviewed journals. I therefore took the results from the micro- and meso scale chapters for the different landscape types, and re-analysed them using the same meta-analytical techniques as in Chapter 6. I refer to the results as a "park effect" and present the results in Appendix C (Fig. 7.1). In this re-analysis, I did not specifically control for elephant presence as I did in the previous chapters, and used the differences in all the responses variables between inside and outside the Park. The overall effect size was significantly negative ($d = -0.24 \pm 0.01$, $p < 0.05$, 95% CI: -0.43 to -0.05, $k = 45$). The open woodland dominated this overall effect and was significantly negative ($d = -0.39 \pm 0.02$, $p < 0.05$, 95% CI: -0.66 to -0.11, $k = 21$). Note that the effect size was not significant in the closed woodland and sand forests, that is, the 95% confidence interval overlapped with zero (for closed woodland: $d = -0.17 \pm 0.02$, $p < 0.05$, 95% CI: -0.44 to 0.10, $k = 21$; sand forests: $d = 0.24 \pm 0.14$, $p < 0.05$, 95% CI: -0.49 to 0.96, $k = 3$ respectively). If the conservation goal was to maintain ecological integrity, the Park has a problem that extends beyond elephants (see Chapter 6 and these results; and options for solutions under the next heading). Overall, the sand forests appeared to be intact, and the mixed woodlands seem to be under pressure from not just elephants, but also management policies towards other herbivores, water and fire.

Two closely linked aspects guided me in my conclusion. Firstly, ecological patterns and processes are scale dependant (Lewin 1986; Levin 1992; May 1994) and secondly, elephants do not operate in isolation (e.g. Dublin *et al*. 1990). Other ecological events may either mask or synergistically contribute to the effect elephants have for their environment. At what scale then do we see a signal of impact left by elephants?

My fieldwork in the Park and the meta-analysis of peer-reviewed studies I conducted implies elephant impact is evident at the smaller scales. In the Park, these signals were most prevalent at the local scale, and with the meta-analysis, in the short-term studies. Elephant impact is immediate at the point of "impact" — measuring structural changes will show that. By increasing the time and spatial scale, ecological processes such as other stochastic and deterministic disturbance events, dispersal, meta-population dynamics, competition and predation play a more prominent role, alleviating and compensating, or even masking possible negative effects of elephants.

Management implications

Conservation agencies around the world face a daunting challenge (Pimm *et al*. 2001). When Conservation International proclaimed Maputaland part of a biodiversity hotspot, they highlighted the importance of this region. These hotspots have two criteria, rich in endemic species threatened by high human densities and unsustainable land use practices (Myers *et al*. 2000). Formal conservation areas in these hotspots are therefore particularly important, and sound ecological theory should guide management decisions. Managing Tembe Elephant Park is no exception, and here I will discuss the interpretation of my study results to the management of elephants living in the Park.

Two points need consideration before I proceed. First, from a management point of view, ecosystems are complex and maintained by a range of scale dependant processes (e.g. Levin 1992). Management decisions may therefore, have unpredictable and non-linear outcomes. Secondly, African savannas, typified by dynamic and alternate stable states, can fluctuate between open grasslands, mixed woodlands and forests (Walker & Noy-Meir 1982; Dublin *et al.* 1990; Gillson 2004). Tembe Elephant Park contains an almost full spectrum of these different states, arranged in a heterogeneous and complex mosaic. This may complicate matters, but does not prevent the formulation of a relatively simple management solution for elephants living here.

Until now, the vegetation in the Park shows minimal signs of negative elephant impact. My recommendations may prevent future unacceptable and irreparable damage, before it happens. Elephants affect the open woodlands more than the closed woodlands and sand forests. However, although not investigated here, I cannot exclude the impact of frequent hot fires prevalent in the open woodlands as a contributing factor. Park's management prescribes the burning regime and elephants here thus do not operate in isolation.

If elephant numbers becomes a 'problem', three options are available: do nothing, regulate numbers within predetermined fixed asymptotes or let environmental limitations control their numbers. To do nothing is self-explanatory. Regulating numbers usually takes the form of culling (e.g. Astle 1971; van Aarde *et al*. 1999), translocation (summarised in Garaï *et al*. 2004) or immuno-contraception (Fayrer-Hosken *et al*. 2000; Pimm & van Aarde 2001). These controversial and often sensitive options give a false sense of predictability in their outcomes. Forcing constant values onto elephant population and demographic variables may not have the expected outcomes, such as decreasing population growth rates or stem the degradation of vegetation. Under these scenarios, the fences surrounding the Tembe Elephant Park and the provision of artificial water remain intact. Here in lie clues for the management. The Park still has a low elephant density – but compared to the free roaming elephants in southern Mozambique, already show some aberrant selection to landscapes. I ascribed this to the fences and redistribution of limiting resources such as water. Fences also trap the system into a fixed state that is unnatural for dynamic systems such as savannas. These constrains effectively decrease the scale at which elephants can operate and force agencies to continue their investigation into alternative and adaptive elephant management strategies. A circular argument ensues and spirals into a permanent conservation management predicament.

Elephant management is in dire need of a paradigm shift (similar to Wu & Loucks 1995; Briske *et al.* 2003). This shift should be from a perceived 'balance of nature' to 'flux of nature' by accepting non-linear and unpredictable dynamics (Gillson & Lindsay 2003), stabilised by large-scale processes and structure (Lewin 1986; Western *et al.* 1989; Bulte *et al*. 2004). This gives us a third option in solving this dilemma. If we allow for scale-dependant processes, such as metapopulation dynamics or other spatiotemporal models (Thomas & Kunin 1999) to operate, elephants may have the opportunity to establish sink and source populations through range expansion into marginal areas. In effect, by doing so, restoration principles (e.g. Dobson *et al*. 1997; Young 2000) combined with wildlife management techniques and elephant dispersal could reinstate migration patterns. Under this metaphor, the impact of elephants could be limited on the environment by allowing for the temporal alleviation of relatively high elephant densities. Dispersal in essence, may initiate recovering periods for other parts of the affected system. This argument also gives ecological and scientific impetus for the expansion of conservation areas.

I conclude – conservation managers, in their effort to conserve, enhance and maintain biological diversity, should always attempt to simulate scale-dependant ecological processes. From a philosophical point of view, I define the ‘elephant problem’ now as ‘elephants being the result of a problem’. In addition, I would like to change the underlying statement in the debate, from ‘elephants against diversity’ to ‘elephants are central to biodiversity’.

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Appendix A

The woody species we sampled in the sand forests and mixed woodlands both inside and outside Tembe Elephant Park listed in alphabetical order (Chapters 3 & 4). The values assigned to each species are the ranked position of that species relative to the others in each of the landscapes; the lower the value the higher the species relative abundance. Empty cells imply that the species were not found in that landscape. Species names and authority follows Arnold & de Wet (1993).

			Sand forests		Closed woodland		Open woodland	
	Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
1.	*Acacia burkei*	Benth.	9	68	10	25	2	5
2.	*Acacia karroo*	Hayne				64	39	
3.	*Acacia nilotica*	(L.) Willd. ex Del.			61	57	47	
4.	*Acacia robusta*	Burch.			58	97	15	
5.	*Acalypha glabrata*	Thunb.	36	33	15	40		
6.	*Acridocarpus natalitius*	Juss.	30	35	66	72	33	44
7.	*Afzelia quanzensis*	Welw.	60	69	22	85		

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
8. *Albizia adianthifolia*	(Schumach.) W.F. Wight		63	89	20	25	9
9. *Albizia anthelmintica*	(A.Rich.) Brongn.				106		
10. *Albizia forbesii*	Benth.	73					
11. *Albizia versicolor*	Welw. ex Oliv.			90	51	23	13
12. *Aloe marlothii*	Berger						
13. *Ancylanthos monteiroi*	Oliv.	74		34	76		
14. *Antidesma venosum*	E.Mey. ex Tul.			71	79	34	40
15. *Balanites maughamii*	Sprague	33	13	51	73	48	31
16. *Berchemia zeyheri*	(Sond.) Grubov				90		
17. *Berchemia sp. nov.*		75					
18. *Boscia foetida*	Schinz	40	34	72	68		
19. *Brachylaena discolor*	DC.			36	27	3	20

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
20. *Brachylaena huillensis*	O.Hoffm.	8	49			31	
21. *Bridelia cathartica*	Bertol. f.			13	16	24	12
22. *Calodendrum capense*	(L. f.) Thunb.				98		
23. *Canthium inerme*	(L. f.) Kuntze	44	64	25	45	54	52
24. *Canthium setiflorum*	Hiern	34	22	82	86		
25. *Carissa bispinosa*	(L.) Desf. ex Brenan		65		14	35	
26. *Carissa tetramera*	(Sacleux) Stapf						
27. *Casearia gladiiformis*	Mast.			91			
28. *Cassine aethiopica*	Thunb.			77	69		
29. *Cassine transvaalensis*	(Burtt Davy) Codd			92			
30. *Cassipourea mossambicensis*	(V. Brehm.) Alston	48	38	67			
31. *Catunaregam spinosa*	(Thunb.) Tirvengadum	58	66	3	6	8	8

	Species	Authority	Sand forests		Closed woodland		Open woodland	
			Inside	Outside	Inside	Outside	Inside	Outside
32.	*Chaetacme aristata*	Planch.			93			
33.	*Cladostemon kirkii*	(Oliv.) Pax & Gilg						
34.	*Clausena anisata*	(Willd.) Hook. f. ex Benth.	51	37	9	1	56	
35.	*Cleistanthus schlechteri*	(Pax) Hutch.	22	16	78	92	55	
36.	*Clerodendrum glabrum*	E. Mey.				29	57	45
37.	*Coddia rudis*	(E. Mey. ex Harv.) Verdc.		52	19	3	49	
38.	*Coffea racemosa*	Lour.			83			
39.	*Cola greenwayi*	Brenan	4	5	41	52		
40.	*Combretum mkuzense*	Carr & Retief	28	41		107		
41.	*Combretum molle*	R. Br. ex G. Don			8	15	6	14
42.	*Commiphora neglecta*	Verdoorn	76	48	18	9		19
43.	*Commiphora zanzibarica*	(Baill.) Engl.					42	

	Species	Authority	Sand forests		Closed woodland		Open woodland	
			Inside	Outside	Inside	Outside	Inside	Outside
44.	*Cordia monoica*	Roxb.			49	87		
45.	*Craibia zimmermannii*	(Harms) Dunn	61					
46.	*Crotalaria monteiroi*	Taub. ex Bak. f.						
47.	*Croton pseudopulchellus*	Pax	1	4	12	65		
48.	*Croton steenkampianus*	Gerstner	14	18	73	88	43	
49.	*Cussonia arenicola*	Strey				93		
50.	*Deinbollia oblongifolia*	(E. Mey. ex Arn.) Radlk.	53	54	68	48		53
51.	*Dialium schlechteri*	Harms	31	17	1	10	22	22
52.	*Dichrostachys cinerea*	(L.) Wight & Arn.	68	70	33	12	4	1
53.	*Diospyros dichrophylla*	(Gand.) De Winter			4	13	12	17
54.	*Diospyros inhacaensis*	F. White	45	36	94	99		
55.	*Dombeya cymosa*	Harv.	63					

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
56. *Dovyalis caffra*	(Hook. f. & Harv.) Hook. f.	64		95			
57. *Dovyalis longispina*	(Harv.) Warb.	27	42	42	37		26
58. *Drypetes arguta*	(Müll. Arg.) Hutch.	3	1				
59. *Drypetes gerrardii*	Hutch.		44				
60. *Drypetes natalensis*	(Harv.) Hutch.	24	71	52	80	58	
61. *Ehretia obtusifolia*	Hochst. ex DC.				49	44	46
62. *Ekebergia capensis*	Sparrm.			84	60		
63. *Erythrococca berberidea*	Prain	69	67	55	58		
64. *Erythrophleum lasianthum*	Corbishley	56	46		70	36	
65. *Erythroxylum delagoense*	Schinz				53		27
66. *Erythroxylum emarginatum*	Thonn.	62	55				
67. *Euclea divinorum*	Hiern			45		40	

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
68. *Euclea natalensis*	A. DC.	23	25	2	4	32	6
69. *Euphoria grandidens*	Haw.	70	51				
70. *Euphorbia ingens*	E. Mey. ex Boiss.		72	53	43		
71. *Ficus thonningii*	Blume						
72. *Flueggea verosa*	(Roxb. ex Willd.) Pax & K. Hoffm.						41
73. *Garcinia livingstonei*	T. Anders			56	54	28	37
74. *Gardenia volkensii*	K. Schum.		73		108		47
75. *Grewia caffra*	Meisn.	47	59	23	30	45	48
76. *Grewia flavescens*	Juss.			28		21	
77. *Grewia microthyrsa*	K.Schum. ex Burret	29	47	39	41	9	42
78. *Grewia occidentalis*	L.				109		54
79. *Grewia subspathulata*	N.E. Br.						49

	Species	Authority	Sand forests		Closed woodland		Open woodland	
			Inside	Outside	Inside	Outside	Inside	Outside
80.	*Gymnosporia senegalensis*	(Lam.) Loes			40	39	18	32
81.	*Haplocoelum gallense*	(Engl.) Radlk.	41	10	79	62		
82.	*Harpephyllum caffrum*	Bernh. ex Krauss			96	35		
83.	*Hymenocardia ulmoides*	Oliv.	12	6	38	38	29	34
84.	*Hyperacanthus amoenus*	(Sims) Bridson	77					
85.	*Hyperacanthus microphyllus*	(K. Schum.) Bridson	32	8		66		
86.	*Hyphaene coriacea*	Gaertn.					26	15
87.	*Isoglossa woodii*	C.B. Cl.	10	45				
88.	*Kigelia africana*	(Lam.) Benth.				89		
89.	*Lagynias lasiantha*	(Sond.) Bullock	15	27	31	46	37	18
90.	*Landolphia kirkii*	T.-Dyer	16	7				
91.	*Lannea schweinfurthii*	(Engl.) Engl.		74				

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
92. *Leptactina delagoensis*	K. Schum.			85			
93. *Maerua angolensis*	DC.				110		
94. *Maerua nervosa*	(Hochst.) Oliv.				111		
95. *Manilkara discolor*	(Sond.) J.H. Hemsl.	46	23	44	18		55
96. *Margaritaria discoidea*	(Baill.) Webster	57	60	30	21	50	56
97. *Maytenus undata*	(Thunb.) Blakelock				112		
98. *Memecylon sousae*	A. & R. Fernandes	35	56	54			
99. *Monanthotaxis caffra*	(Sond.) Verdc.	2	3				
100. *Monodora junodii*	Engl. & Diels	21	21		100		
101. *Mundulea sericea*	(Willd.) A. Chev.			97	63	7	38
102. *Newtonia hildebrandtii*	(Vatke) Torre	49	30	74	77		
103. *Ochna arborea*	Burch. ex DC.	65	61				

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
104. *Ochna barbosae*	N.K.B. Robson			62	61		
105. *Ochna natalitia*	(Meisn.) Walp.	19	40	59			
106. *Oxyanthus latifolius*	Sond.	43	43	86	113		
107. *Ozoroa engleri*	R. & A. Fernandes				91	10	10
108. *Pappea capensis*	Eckl. & Zeyh.				101		
109. *Pavetta revoluta*	Hochst.					38	
110. *Pavetta schumanniana*	F. Hoffm. ex K. Schum.			98	11		57
111. *Peltophorum africanum*	Sond.			99			
112. *Phoenix reclinata*	Jacq.						
113. *Phyllanthus reticulatus*	Poir.				78		24
114. *Plectroniella armata*	(K. Schum.) Robyns			50	44		
115. *Psydrax locuples*	(K. Schum) Bridson	13	15	5	8	30	25

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
116. *Ptaeroxylon obliquum*	(Thunb.) Radlk.	25	32	35	94	59	50
117. *Pteleopsis myrtifolia*	(Laws.) Engl. & Diels	18	19	46	32	60	51
118. *Rhoicissus digitata*	(L. f.) Gilg & Brandt				102		
119. *Rhus gueinzii*	Sond.	54	57	20	42	14	29
120. *Rothmannia fischeri*	(K. Schum.) Bullock	20	24	69	81		
121. *Salacia leptoclada*	Tul.	5	14	87			
122. *Sapium integerrimum*	(Hochst.) J. Leonard	59		21	26	19	35
123. *Schotia brachypetala*	Sond.			63	82		
124. *Sclerocarya birrea*	(A.Rich.) Hochst.			80	83	27	16
125. *Scolopia zeyheri*	(Nees) Harv.				19		
126. *Scutia myrtina*	(Burm. f.) Kurz				95		
127. *Senna petersiana*	(Bolle) Lock				114	51	

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
128. *Sphedamnocarpus pruriens*	(Juss.) Szyszyl.						
129. *Spirostachys africana*	Sond.	71		11	24	16	21
130. *Strychnos decussata*	(Pappe) Gilg	37	28	27	28		
131. *Strychnos henningsii*	Gilg	26	11	100	50		
132. *Strychnos madagascariensis*	Poir.			16	2	5	2
133. *Strychnos spinosa*	Lam.		75	7	5	20	3
134. *Suregada africana*	(Sond.) Kuntze		29	88		61	
135. *Suregada zanzibariensis*	Baill.	39		75	103	62	
136. *Synaptolepis kirkii*	Oliv.	11	12				
137. *Tabernaemontana elegans*	Stapf	72	76	14	34	17	11
138. *Tarenna junodii*	(Schinz) Brem.				96		
139. *Tarenna littoralis*	(Hiern) Bridson			47			

		Sand forests		Closed woodland		Open woodland	
Species	Authority	Inside	Outside	Inside	Outside	Inside	Outside
140. *Tarenna supra-axillaris*	(Hemsl.) Brem.	38	20	43	23		58
141. *Teclea natalensis*	(Sond.) Engl.			76	74		
142. *Tecomaria capensis*	(Thunb.)						
143. *Terminalia sericea*	Burch. ex DC.			32	17	1	4
144. *Thespesia acutiloba*	(Bak. f.) Exell & Mendonca				104	52	
145. *Toddaliopsis bremekampii*	Verdoorn	6	2				
146. *Trema orientalis*	(L.) Blume				67		
147. *Tricalysia africana*	(Sim) Robbrecht	66					
148. *Tricalysia capensis*	(Meisn. ex Hochst.) Sim	67	50	64	55		
149. *Tricalysia delagoensis*	Schinz	42	26	26	71		
150. *Tricalysia junodii*	(Schinz) Brenan	7	9		56		
151. *Tricalysia lanceolata*	(Sond.) Burtt Davy			17	84		

Species	Authority	Sand forests		Closed woodland		Open woodland	
		Inside	Outside	Inside	Outside	Inside	Outside
152. *Trichilia emetica*	Vahl			101	22	53	28
153. *Uvaria caffra*	E. May. ex Sond		77				
154. *Vangueria cyanescens*	Robyns			81	105	46	36
155. *Vangueria infausta*	Burch.			48	36	13	7
156. *Vepris lanceolata*	(Lam.) G. Don	17	62	6	31	63	43
157. *Vernonia colorata*	(Willd.) Drake			57		64	
158. *Vitex amboniensis*	Guerke		53				
159. *Vitex obovata*	E. Mey.	50		65	33	41	59
160. *Wrightia natalensis*	Stapf	52	31		115		
161. *Ximenia caffra*	Sond.	78		70	59		39
162. *Xylotheca kraussiana*	Hochst.		58	60	7		33
163. *Zanthoxylum capense*	(Thunb.) Harv.	55	39	24	47	65	23

Species	Authority	Sand forests		Closed woodland		Open woodland	
		Inside	Outside	Inside	Outside	Inside	Outside
164. *Ziziphus mucronata*	Willd.			37	75	11	30

Appendix B

Alphabetical list of the peer-reviewed articles used in the meta-analysis in Chapter 6.

Afolayan, T.A. (1973) The ecological problems facing a wildlife manager in east Africa: possible solutions to similar problems in Nigeria. *The Nigerian Journal of Forestry*, **3**, 21-25.

Afolayan, T.A. (1975) Effects of elephant activities on forest plantations in the Kilimanjaro forest-game reserve in northern Tanzania. *Oikos*, **26**, 405-410.

Afolayan, T.A. (1976) Habitat utilisation by elephant in the Guinea zone. *Commonwealth Forestry Review*, **55**, 65-71.

AfESG. (1994) Working group discussion three - Elephant – Habitat Working Group. *Pachyderm*, **18**, 10-18.

Agnew, A.D.Q. (1968) Observations on the changing vegetation of Tsavo National Park (East). *East African Wildlife Journal*, **6**, 75-80.

Anderson, G.D. & Walker, B.H. (1974) Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the southern African Wildlife Management Association*, **4**, 1-14.

Augustine, D.J. & McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, **62**, 1165-1183.

Augustine, D.J. & McNaughton, S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, **41**, 45-58.

Bainbridge, W.R. (1965) Distribution of seed in elephant dung. *Puku*, **3**, 173-175.

Barnes, M.E. (2001a) Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments*, **49**, 541-554.

Barnes, M.E. (2001b) Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*, **39**, 340-350.

Barnes, R.F.W. (1980) The decline of the baobab tree in Ruaha National Park, Tanzania. *African Journal of Ecology*, **18**, 243-251.

Barnes, R.F.W. (1983a) The elephant problem in Ruaha National Park, Tanzania. *Biological Conservation*, **26**, 127-148.

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Bell, R.H.V. (1985) Elephants and Woodlands – a reply. *Pachyderm*, **5**, 17-18.

Belsky, A.J. (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology*, **22**, 271-279.

Ben-Shahar, R. (1993) Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*, **65**, 249-256.

Ben-Shahar, R. (1996a) Woodland dynamics under the influence of elephants and fire in northern Botswana. *Vegetatio*, **123**, 153-163.

Ben-Shahar, R. (1996b) Do elephants over-utilize mopane woodlands in northern Botswana? *Journal of Tropical Ecology*, **12**, 505-515.

Ben-Shahar, R. (1997) Elephants and woodlands in northern Botswana: how many elephants should be there? *Pachyderm*, **23**, 41-43.

Ben-Shahar, R. (1998a) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*, **136**, 189-194.

Ben-Shahar, R. (1998b) Elephant density and impact on Kalahari woodland habitats. *Transactions of the Royal Society of South Africa*, **53**, 149-155.

Birkett, A. (2002) The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology*, **40**, 276-282.

Botha, J., Witkowski, E.T.F. & Shackleton, C.M. (2002) A comparison of anthropogenic and elephant disturbance on *Acacia xanthophloea* (fever tree) populations in the Lowveld, South Africa. *Koedoe*, **45**, 9-18.

Bowland, J.M. & Yeaton, R.I. (1997) Impact of domesticated African elephants *Loxodonta africana* on Natal Bushveld. *South African Journal of Wildlife Research*, **27**, 31-36.

Brahmachary, R.L. (1980) On the germination of seeds in the dung balls of the African elephant in the Virunga National Park. *La Terre et la Vie*, **34**, 139-142.

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Buss, I.O. (1977) Management of big game with particular reference to elephants. *The Malayan Nature Journal*, **31**, 59-71.

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Appendix C

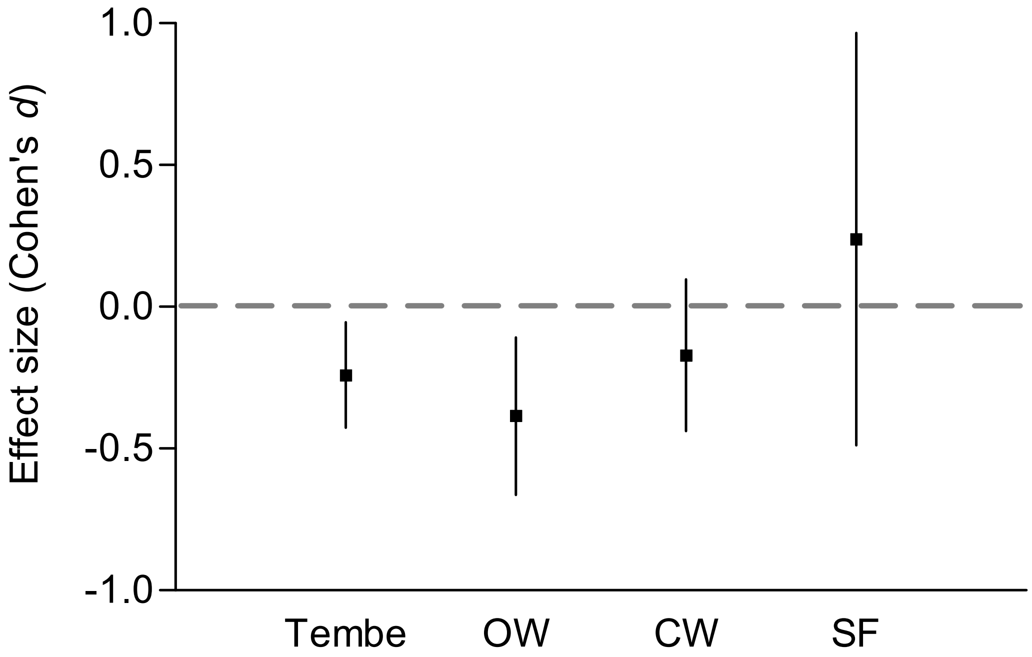

Fig. 7.1 The overall effect size (using the Cohen's *d* statistic) is significantly negative (the 95% confidence interval does not overlap with the zero dashed line) for Tembe Elephant Park. The open woodlands (OW) in the Park contributed mostly to this overall negative effect, with the closed woodlands (CW) and sand forests (SF) showing non-significant effect sizes (see text in Synthesis for details).